The ecology of the butterfish *Odax pullus* around the Kaikoura Peninsula

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Dark-heaving-boundless,
endless and sublime

The image of eternity

(Lord Byron, 1818)

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This study examines the abundance, distribution, reproduction and feeding behaviour of the *Odax pullus* (butterfish) around the Kaikoura Peninsula. *O. pullus* is one of a small number of species of herbivorous fish inhabiting temperate marine waters and is one of only two herbivorous species that are widely distributed in New Zealand and extend their ranges into cold southern latitudes. In this study, the abundance of butterfish across habitats and depths, and associations with other mobile reef fish species, were examined monthly for thirteen months. This enabled a determination of the spatial and temporal variability of butterfish populations. Visual underwater transects at nine sites showed that butterfish were associated exclusively with habitats dominated by large brown algae, particularly *Lessonia variegata*, *Marginariella boryana* and *Carpophyllum* spp. Abundance declined during winter, probably because larger fish migrated into deeper reef habitats. Recruitment occurred during summer. Butterfish are wide-ranging along the patch reefs around Kaikoura and there were no marked differences in the depth distribution of the different ontogenetic stages.

Histological examination of gonads was used to determine sex, minimum size to reproduction, reproductive seasonality and length of the spawning season. Butterfish are reproductive from July to December, with peak gonad ripeness occurring in September and October. There was a clear separation between sizes of female and male fish. No individuals < 370 mm SL, but all of those above this size, were males. This is suggestive that *O. pullus* is a protogynous hermaphrodite, which was further supported by the histological examination of gonads. Nine testes in fish > 380 mm SL contained both sperm and retained eggs. Nineteen female butterfish reached maturity at around 200 mm SL, which is smaller than found in earlier studies in the North Island. Scales and otoliths were used to estimate age. The number of distinct rings in these structures agreed well until the age six years, after which scales tended to under-estimate age. Despite the distinct size separation of female and male fish, the two sexes overlapped in ages over years 4 - 6. However, most of the oldest fish were males. Butterfish appear to be a fast-growing, relatively short-lived species that reaches a maximum age of around ten years. Very similar colour patterns of larger females and males indicated that visual sexing is often not accurate and, therefore,

histological examination of the gonads is necessary to determine sex reliably, at least for larger individuals.

Gut contents were analysed to determine the diet of butterfish and how it compared to findings of studies done in the North Island. The latitudinal change in the species mix of dominant large brown algae is reflected in the diet of *O. pullus*. Around Kaikoura, butterfish feed predominantly on the laminarian *Lessonia variegata* which is very abundant in subtidal habitats. Butterfish in northern New Zealand feed predominantly on *Ecklonia radiata* and *Carpophyllum* spp. This latitudinal diet shift indicates that butterfish are highly adaptable in their feeding habit. Furthermore, a small proportion of butterfish (6.5 %) targeted salps in their feeding. The presence of animal material in the gut contents of herbivorous fish has usually been ascribed to incidental feeding, but it is clear that this feeding is both opportunistic and selective in butterfish populations around Kaikoura.

Spawning and its associated behaviours were not seen during this study, probably because they occur either in open water or else on deeper reefs. However, the sex distribution in *Odax pullus* indicates that this species has a complex social system and there is clear evidence of male territoriality during the reproductive period. There is considerable fishing pressure on butterfish populations around Kaikoura, which targets mostly larger fish. Despite this, the populations around Kaikoura seem to be robust. Butterfish have only a moderate life span for an inshore fish, but there are many juveniles in the local populations, indicating that there was successful recruitment for at least a few years.

CHAPTER ONE

General Introduction

1.1 GENERAL BIOLOGY

The family Odacidae is comprised of twelve species of morphologically diverse fish inhabiting the shallow temperate and subtemperate marine waters of Australia and New Zealand (Gomon & Paxton, 1986). Cuvier (1829) was one of the first to note their close relationship with the Labridae, a family including approximately 600 species in temperate and tropical waters. Three distinct morphological features, however, necessitated the formation of a separate family for this assemblage (Gomon & Paxton, 1986). The features were the fusion of the jaw teeth into beak-like cutting plates, the high number of dorsal spines and the presence of only four rays in the ventral fins. One exception to this is *Siphonognathus argprophanes* where the ventral fins are absent (Gomon & Paxton, 1986).

Although the Odacidae include twelve species, the New Zealand marine fauna contains only two representatives, *Odax cyanoallix* Ayling & Paxton, 1983 and *Odax pullus* (Schneider, 1801). While *O. cyanoallix* is restricted to the warmer waters of Northland and the Three Kings Islands (Ayling & Paxton, 1983), *O. pullus* occurs around the entire New Zealand coast including the Snares Islands, Stewart Island, Bounty and Antipodes Islands and the Chatham Islands (Paul, 1986; Francis, 1988, 1996). Butterfish have not been recorded at the subtropical Kermadec Islands (Schiel *et al.*, 1986, Francis *et al.*, 1987). Whitley (1964) indicated the presence of *O. pullus* in Australia, but other studies, such as Gomon & Paxton (1986), failed to find Australian specimens of this species.

O. pullus is a uniquely green-boned species, which has been mentioned in numerous early studies. Apart from Graham (1956), most studies consist only of listings or brief notes (Paul, 1997). Due to the high degree of dichromatism between the ontogenetic stages (Plate 1.1), butterfish appear throughout the early literature as two separate species, *Odax vittatus* Richardson, 1842 (the juvenile) and *Caridodax pullus* Foster, 1801 (the adult).

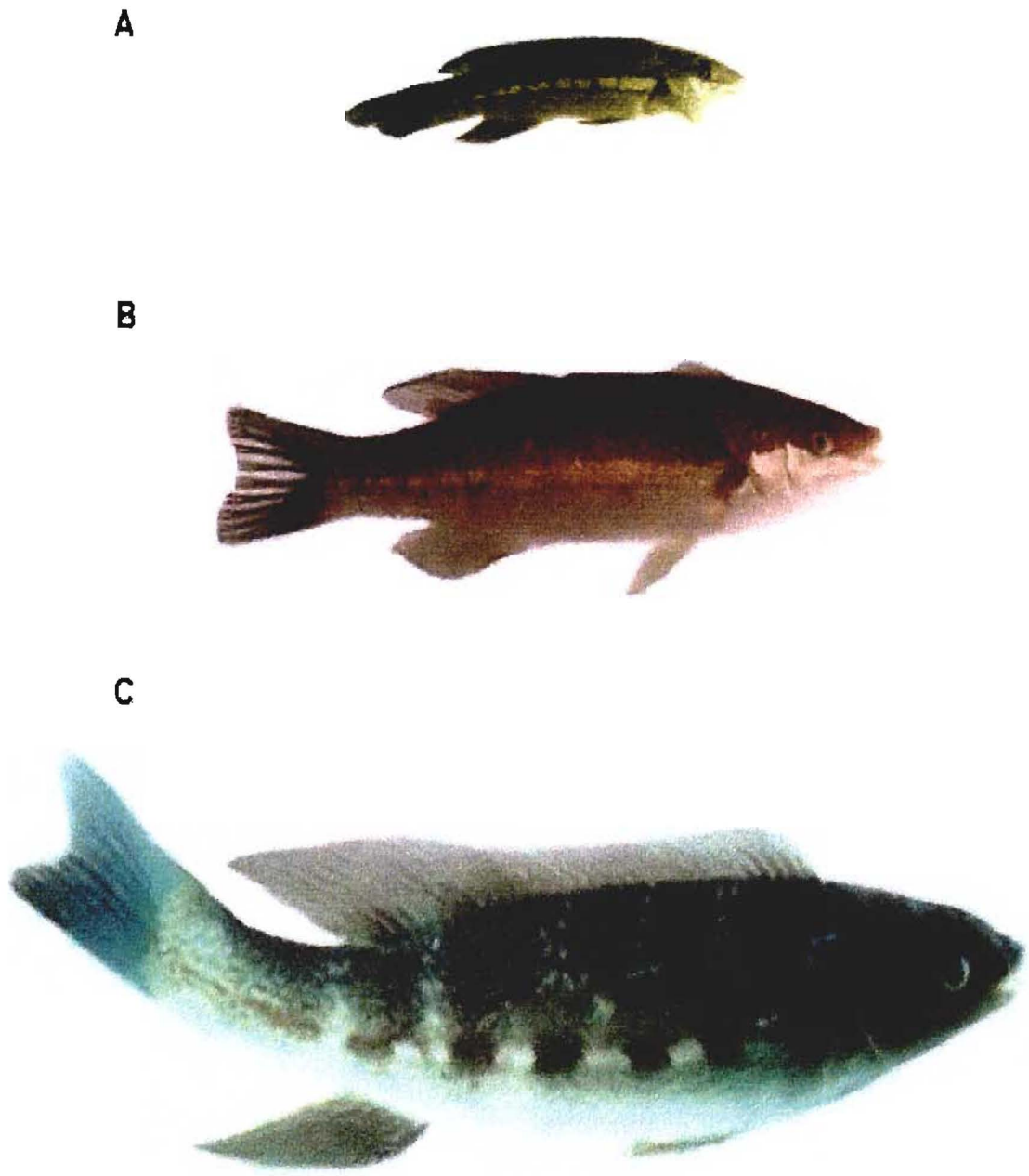


Plate 1.1. The three different ontogenetic stages of *Odax pullus*

A = juvenile; **B** = female; **C** = male

To date, the most comprehensive study on *O. pullus* was by Ritchie (1969), who investigated the general biology of Cook Strait populations. Gomon & Paxton (1987) extended studies on the systematics in their revision of the Odacidae. Most other studies have focused on the feeding ecology and physiology of butterfish (Choat & Ayling, 1987; Clements, 1985, 1991; Clements & Bellwood, 1988; Choat & Clements, 1992, 1993; Clements & Choat, 1993; Meekan, 1986) and only one has looked at reproductive aspects (Crabb, 1993). Paul (1997) provided a detailed summary of the biology and commercial stock landings of *O. pullus*, but due to the lack of available data failed to provide information about stock sizes and structures. With the exception of Meekan (1986), Hickford & Schiel (1995) and Meekan & Choat (1997), no in-depth information is available about the distribution and abundance of butterfish.

Butterfish are believed to be a true cold water species, rather than one of subtropical origin extending its range into southern waters (Choat & Clements, 1992). Adults average around 45-55 cm in length, but maximum sizes of 70-75 cm have been recorded from the southern regions of New Zealand (Doak, 1972; Ayling & Cox, 1987). Butterfish can weigh up to 3.6 kg (Doak, 1972), but usually average about 1.1 kg at around 45 cm SL (Ritchie, 1969). They occur in shallow waters wherever large brown algae are abundant (Ritchie, 1976), with their main habitat being within the moderately turbulent zones of shallow areas (Meekan & Choat, 1997). Butterfish are usually found from the immediate subtidal zone down to a depth of about 20 metres, but there may be a latitudinal trend for *O. pullus* to inhabit deeper waters towards the south. Paul (1997) noted that butterfish seem "to have a shallower depth range in the north (to 10 m) than in Cook Strait (to 20 m) and southern waters (to 40 m)".

Southern waters are also believed to harbour the greatest abundance of butterfish (Doak, 1972). Choat & Ayling found the highest number of *O. pullus* (18.7 per 500 m^2) at sites with greatest latitude (41 °S). Schiel (unpublished data) recorded even greater abundances (29 per 500 m^2) further south (44 °S). However, even though *O. pullus* appear to prefer cold water habitats, they are not found around the subantarctic

Auckland Islands at 50 °S (Kingsford *et al.*, 1989). The increased abundance of butterfish around central and southern New Zealand probably explains the greater commercial and recreational catches in these areas (Plate 1.2).

Plate 1.2. Cumulative reported catches (t) of *O. pullus* for the fishing years 1983-84 to 1987-88, by fishing return statistical areas. Modified from Paul (1997)

Butterfish have been caught commercially and recreationally for well over a century, with landing estimates dating back to 1935 (Paul, 1997). Commercially they are taken almost exclusively by set nets within shallow, algal covered reefs. The main and most stable fishery is located around Cook Strait, between Tasman Bay, Castlepoint and Kaikoura, with annual landings ranging from 100 to 200 t between the early 1980's and 1995 (Annala & Sullivan, 1996). A smaller fishery also occurs around the Southland coast and Stewart Island. Commercial landings usually peak during the winter, suggesting that some local fishers alternate between crayfish potting in the summer and butterfish netting in the winter (Ritchie, 1969). The recreational fishery is more important within the warmer months of the year, but the overall catch is likely to be similar to the commercial catch. *O. pullus* are very popular with recreational fishers in many parts of New Zealand, and were fished by coastal Maori tribes (Knox, 1871). In addition to set nets, they are also taken by spear-fishing.

1.1.1 Reproduction

The reproductive biology of many labroid species is well known and has been the subject of intense studies (e.g. Bolin, 1930; Robertson, 1972; Robertson & Choat 1974; Robertson & Warner, 1978; Warner & Robertson, 1978, Warner & Lejeune, 1985, Martel & Green, 1987; Dipper & Pullin, 1979; Jones, 1980; 1981a,b; Gillanders 1995a). The reproductive patterns of *Odax pullus*, however, are still relatively unknown, with only two studies focussing on this subject (Ritchie, 1969; Crabb, 1993). Similar to labrids, butterfish are believed to be sequentially hermaphroditic, evidence of which was first provided by Graham (1939; 1956) and later strongly supported by Ritchie (1969; 1976) and Crabb (1993).

Sex reversal appears to be a common feature in Odacids (Gomon & Paxton, 1986) and in labrids from the Southern Hemisphere (Thompson, 1981). Hermaphroditic species exhibit both functional male and female gonads during their life history.

Protandrous hermaphrodites first pass through the male stage, whereas protogyny describes the opposite condition (Crabb, 1993). During sex reversal, individuals undergo irreversible changes in gonad function and anatomy (Cole, 1990; Cardwell & Liley, 1991).

Anatomical changes in *Odax pullus* during sex reversal result in a conspicuous dimorphism between the sexual stages (Ritchie, 1976). One distinct feature is the change in form and body shape. Juveniles have a slender body which deepens with increasing size and age. Large adults, in particular males, have longer anal and dorsal fins. With increasing age, butterfish also exhibit distinct changes in head shape. There is a notable increase in the snout angle, from around 30° in small juveniles (> 100 mm) to more than 60° in large adults. This is based on the proportional increase in cheek depth (Clements, 1985). There does not appear to be a proportional increase in snout length with size (Clements, 1985).

This body transformation with increasing size is accompanied by considerable differences in colouration. Small juveniles possess a reddish brown colour with a pale mid-body stripe. With increasing size their colour turns into a golden yellow and the stripe becomes darker. At around 30 cm juveniles turn into females, which are characterised by a brown-greenish colouration. When reaching approximately 40 cm, about half of the females are believed to transform into males showing a very dark, almost black dorsal and a light olive green ventral region (Paul, 1997). The lateral stripe becomes increasingly broken and less distinct in larger fish. In addition, males also exhibit bright fin marks. Within the reproductive season, both sexes also develop distinct blue chin markings.

Odax pullus have a long spawning season, which is believed to extend from July to March, peaking in September-October and December-January (Ritchie, 1969). Peak spawning time may have regional differences. Robertson (1973) suggested that the spawning season in southern waters was shorter, because of the colder temperatures.

This was supported by Crabb (1993) who found that the spawning season for populations around the Otago Peninsula lasted from August to January. During the reproductive season, butterfish function as partial spawners, releasing several batches of up to 6000 eggs (Paul, 1997), with a total fecundity of up to 389000 eggs per fish in the Cook Strait region (Ritchie, 1969). Similar to most other reef fish, butterfish have planktonic eggs and larvae (Robertson, 1973, Dolphin, 1997). However, Ritchie (1969) suggested that they only have a very short planktonic larval stage, leaving the plankton soon after hatching and recruiting into nearshore algal stands.

1.1.2 Feeding

Butterfish are one of six marine reef fish in New Zealand waters with a predominantly herbivorous diet (Ayling & Paxton, 1983). In contrast to their close herbivorous relatives, the labrids and scarids, they do not possess a pharyngeal grinding apparatus. *O. pullus* compensate for this absence by having endosymbiotic communities of bacteria in the distal end of the gut that digest the cellulose of the ingested macroalgae (Clements, 1991).

Butterfish can be classified as facultative herbivores (Choat & Clements, 1992), feeding mainly on *Macrocystis* pyrifera, *Ecklonia radiata* and *Carpophyllum* spp. (Horn, 1989). This preference for large laminarians and fucoids stands in contrast to most other New Zealand herbivorous fish. Marblefish, *Aplodactylus arctidens*, hiwihiwi, *Chironemus arctidens*, and parore, *Girella tricuspidata*, feed mainly on smaller, finer algae (Paul, 1997).

There may be geographic variations in the diet of butterfish, depending on the regional abundances of algae (Choat & Clements, 1992). *O. pullus* also consume some animal matter, such as worms, crustaceans and salps, but it is unclear whether

this material is actively targeted or taken incidentally with ingested seaweed.

1.2 Central aims of this thesis

Most studies on *Odax pullus* have been done around the north-eastern coast of the North Island. Little is known about the abundance, distribution and biology of butterfish south of Wellington. Therefore, this study aimed to extend the present knowledge by investigating various aspects of the biology of this species around the Kaikoura Peninsula.

The Kaikoura Peninsula is located on the northeast coast of the South Island between latitudes 42^0 25' 11" and 42^0 23' 22" (Plate 1.3). It projects approximately four kilometres from the Marlborough coast.

Plate 1.3 Aerial view of the Kaikoura Peninsula

One of the unique features of this peninsula is its close proximity to the continental shelf. Approximately five kilometres offshore there is a sharp drop from 100 to 500 metres to the continental slope, which rises from the southern extremity of the Kermadec Trench (Rasmussen, 1965). Along the trench, upwelling currents transport nutrient-rich waters to the surface layers. The region is strongly influenced by both warm currents from the north and cold currents from the south.

Kaikoura is situated at the northernmost point of the subtropical convergence zone, where the cold sub-antarctic Southland Current meets the warmer subtropical East Cape Current (Heath, 1985) (Plate 1.4).

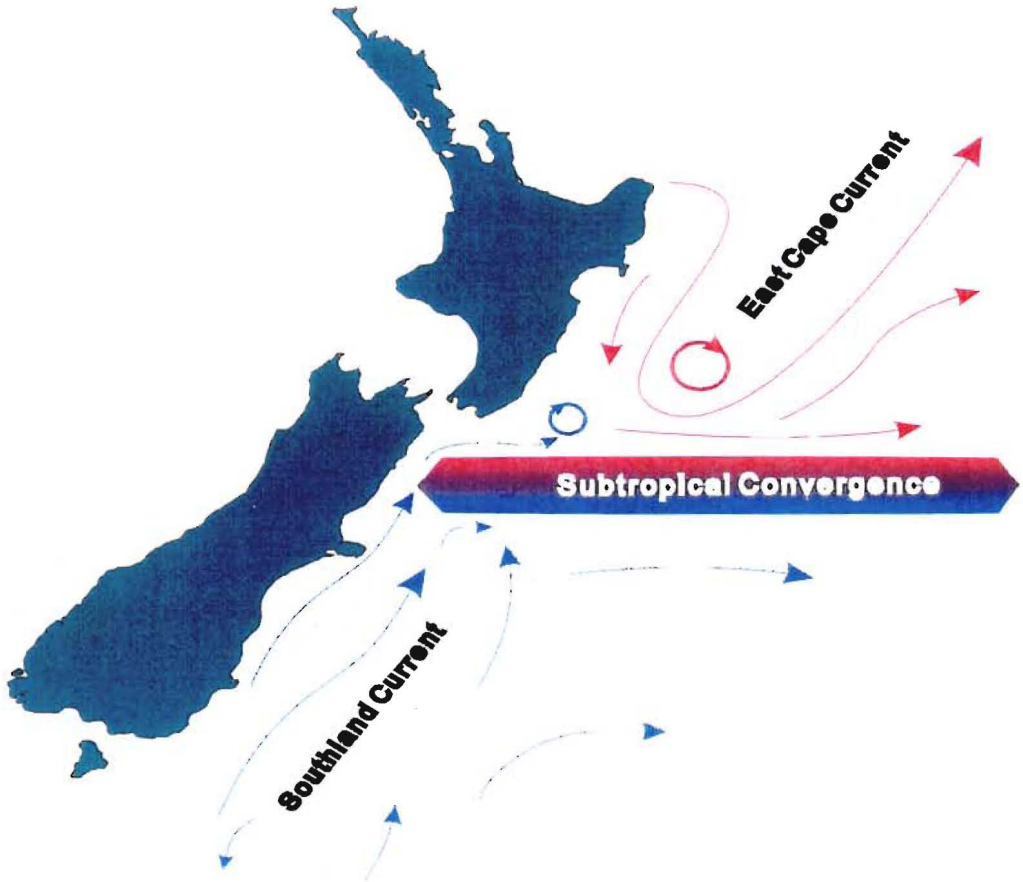


Plate 1.4 Schematic diagram of the subtropical convergence and the involved currents. Modified from Anon. (1997 b)

Although the convergence strongly influences the marine environment around Kaikoura, the relative importance of each current varies seasonally. The coastline is frequently exposed to high energy oceanic swells and storm waves (Rasmussen, 1965), with southerly winds predominating in winter and northerlies in summer (Williams, 1990). In winter, the increased frequency and strength of southerly winds promote the onshore transport of colder water. During summer, however, the northerly winds increase the introduction of warm water from the East Cape Current (Heath, 1972). Because of these seasonal differences, the waters around Kaikoura exhibit inshore temperatures that range from 8.5°C to 19°C (Ottaway, 1976; Pirker, 1992). As a result, the coastal waters and rocky reef habitats of Kaikoura mark the approximate distributional limits of many northern and southern marine species (Knox, 1960).

Although not as diverse as their tropical counterparts, temperate rocky reefs support a variety of reef fish species. However, there is a limited amount of literature available on the ecology of reef fish in New Zealand (see Choat, 1982 and Jones, 1988 for review). With the exception of Crabb (1993) and Hickford & Schiel (1995), most of these studies have focussed on the association of fish assemblages with reef habitats within the warmer waters of the North Island (Russell, 1971; Jones & Thompson, 1980; Leum & Choat, 1980; Jones, 1980, 1981a,b,c, 1984 a,b; Meekan, 1986; Choat *et al.*, 1988; Connell & Jones, 1991). Therefore, very little is known about the abundance, distribution and habitat association of reef fish along the southeast coast of New Zealand.

Reef fish are known to be closely associated with the physical and biological features of reefs (Kingett & Choat, 1981; Choat & Ayling, 1987; Carr, 1994). Because of this close association, habitat complexity, substrate type and algal abundance are believed to play a major role in structuring reef fish communities. Therefore, any changes in these habitat characteristics are likely to affect the composition and abundance of the assemblages (Choat & Ayling, 1987).

The nearshore reef habitats of New Zealand are dominated by large stands of macroalgae which, as elsewhere, provide shelter (Barnes & Hughes, 1982; Anderson, 1994), food (Carr, 1991a; Choat & Clements, 1992), spawning sites (Holbrook *et al.*, 1994) and recruitment habitats (Choat, 1982; Carr, 1994). Algal assemblages are subject to considerable spatial and temporal variation (Schiel & Foster, 1986), which in turn is likely to affect the composition and abundance of the local reef fish assemblage (Carr, 1989; DeMartini & Roberts, 1982). However, variability in the abundance and diversity of fish species can be observed in a variety of habitats, ranging from coral reefs in tropical waters (Choat & Bellwood, 1985) to cold subantarctic habitats (Kingsford *et al.*, 1989).

The composition of a fish assemblage at any point in time and at any given location, can be seen as the result of a series of filters (Tonn *et al.*, 1990). The high variability of abiotic and biotic factors between locations, therefore, necessitates the study of local assemblages, in order to extend the knowledge of the ecology of reef fish in New Zealand (Chapter 2).

Knowledge of the reproductive patterns and cycles of a species is essential to the understanding of its ecology. The reproductive strategy of a fish species can be very complex, comprising various traits designed to ensure maximum survival of offspring. Such traits include the age at first reproduction, size and age related fecundity, characteristics of the gametes, degree of sexual parity, timing of the reproductive season and, in some species, sex change (Wootton, 1984). To extend the present knowledge on butterfish reproduction, some of the key aspects are examined (Chapter 3).

Feeding behaviour and diet is another important component of the ecology of a species. Because there is no detailed information available on feeding of butterfish in the South Island, this was assessed to gain an insight into latitudinal variations and their link to differences in seaweed abundances (Chapter 4).

The diversity of body shapes, habitat preferences and feeding preferences is matched by the diversity of life-history patterns and behaviours (Breder & Rosen, 1966; Balon, 1975). These traits and behaviours are all designed to maximise fitness and survival of the individuals within each species. To describe the ecology of butterfish thoroughly, therefore, it is necessary to gain a better understanding about their behaviour and social systems (Wootton, 1992) (Chapter 5).

By investigating the abundance, distribution, reproductive strategies and traits, feeding and dietary preferences and behaviour, this study aims to extend the present knowledge of the ecology of *Odax pullus*. By investigating populations in central New Zealand, latitudinal aspects and variation can be compared with other areas where studies have been done. This will provide a more general insight into the life of this unique species.

CHAPTER TWO

Reef fish assemblages

2.1 Introduction

2.1.1 Fish and habitat association

Temperate reef fish assemblages are composed of a great variety of species representing a wide range of body sizes, life histories, trophic relations and other ecological characteristics (Holbrook *et al.*, 1994). In New Zealand, the distribution and abundance of these assemblages are strongly influenced by ocean currents (Francis, 1996). The Antarctic Convergence determines the distinctly subantarctic fauna around the Auckland Islands (Kingsford *et al.*, 1989), whereas the East Auckland current transports subtropical migrants into the warmer habitats of the North Island and the adjacent islands (Schiel *et al.*, 1986). All species, however, depend on the characteristics of their reef environment.

The physical and biological features of a reef habitat, such as substrate type, complexity and algal cover appear to have a major influence in structuring reef communities (Kingett & Choat, 1981; Jones, 1984 a,b; Carr, 1994). Habitat complexity can be an important factor in determining the diversity and abundance of reef fish assemblages. Structurally complex habitats support more species and individuals than more uniform habitats (Luckhurst & Luckhurst, 1978; Leum & Choat, 1980; Choat & Ayling, 1987; Bodkin, 1988; Carr, 1991 b; Lincoln-Smith & Jones, 1995). Moreno & Jara (1984) found that complex rocky substrata supported a greater number of species because they provided more shelter and protection from predators than sandy habitats. Connell & Jones (1991) found greater abundances and better survival of the variable triplefin *Forsterygion varium* in areas with complex reef structures.

The complex rocky substratum of temperate reefs not only provides a suitable habitat itself but also supports stands of macroalgae, the presence of which provides additional vertical habitat and shelter while attenuating wave action (Quast, 1968; Mork, 1996). Many reef fish, especially juveniles, show a very close association with macroalgae (Jones, 1984 b,c; Holbrook *et al.*, 1990; Carr, 1991 b). Anderson (1994) found that adult densities of the kelp perch *Brachyistius frenatus* correlated positively

with algal cover. Throughout their life history, these fish are closely associated with macroalgae, especially *Macrocystis* pyrifera, which provides shelter from predators.

Macroalgae, along with associated species, provide a rich source of food for many reef fish (Schmitt & Holbrook, 1986). Choat & Ayling (1987) found a positive correlation between the numbers of common wrasse, *Notolabrus celidotus*, and the abundance of macroalgae. This wrasse feeds on invertebrates (bivalves, crabs and limpets) which are most abundant in macroalgal-dominated habitats (Jones, 1984b; 1984c). Wheeler (1980) suggested that the ingestion of algal material by most fish in temperate waters is only incidental to consumption of animal matter. More recent studies, however, have shown that some species are exclusively herbivorous (Meekan, 1986). Two species commonly observed in southern New Zealand, the marblefish *Aplodactylus arctidens* and the butterfish *Odax pullus*, are believed to feed entirely on algal material (Clements & Bellwood, 1988).

Odax pullus uses macroalgae not only as a food source but also as recruitment habitat. Meekan (1986) found that juvenile butterfish recruit exclusively into stands of the kelp *Ecklonia radiata*. Macroalgae provide recruitment habitats and nursery grounds for many other reef fish (Choat, 1982; Holbrook & Schmitt, 1988). Species such as spotties, *Notolabrus celidotus*, and leatherjackets, *Parika scaber*, have been shown to recruit into macroalgal habitats (Jones, 1984a, Francis, 1988).

The shallow habitats of the northeast coast of the South Island are biologically and topographically more diversified than their North Island counterparts. Individual habitats along the northeast coast of the South Island are often small (less than 100 m^2) and may vary considerably over only a few metres. In Kaikoura, as in north-eastern New Zealand (Choat & Schiel, 1982), the greatest abundance and largest biomass of algae is found in waters shallower than 8 m. However, the echinoid-dominated areas of northern New Zealand (Schiel, 1988) are absent from the habitats of the South Island. The most abundant species in the deeper reef zone of northern New Zealand, *Ecklonia radiata*, is replaced by forests of the large fucoid *Marginariella boryana* along the Kaikoura coast.

All studies describing various aspects of the biology of *Odax pullus* have demonstrated their close association with stands of macroalgae (Meekan, 1986; Clements & Bellwood, 1988, Crabb, 1993). Most of these studies, however, have been done north of Wellington. Meekan (1986) found that, within the Leigh Marine Reserve, butterfish are usually associated with their major food plant, *Ecklonia radiata*. However, this kelp is sparsely distributed around Kaikoura. Meekan (1986) also showed *E. radiata* to be the preferred settlement alga for newly recruited butterfish. Hence, the close association of *Odax pullus* and *Ecklonia radiata* in the North Island appears to be continual throughout their whole life. Hickford & Schiel (1995) determined that around the Kaikoura Peninsula, butterfish are found only in areas with dense algal cover. Because of the difference in algal abundance and diversity between the North and South Island, *O. pullus* may exhibit associations with different algal species. Ritchie (1976) suggested that butterfish gradually migrate into deeper waters with increasing size and, therefore, into areas with different seaweeds. This may affect the fish-algae association through time.

2.1.2 Spatial and temporal variation in fish abundance

Holbrook *et al.* (1994) stated that fish species richness and individual abundance will vary within and among reefs depending on the temporal or spatial scale considered. Several studies have shown marked differences in species densities at a variety of spatial scales, ranging from localities within sites (M°Cormick, 1986) to broad geographic scales (Choat & Ayling, 1987). These species-specific differences in abundance have been correlated with a variety of physical and biological factors (Jones, 1988) (Table. 2.1).

Table 2.1 Significant correlations between reef fish abundance and habitat covariates from medium-scale studies in north-eastern New Zealand. (ρ, Pearsons correlation coefficient). Reproduced from Jones (1988) Table 2

Species	Family	Category	Covariate	ρ	Reference
Cheilodactylus spectabilis	Cheilodactylidae	All	Topographic complexity	0.88	Leum & Choat (1980)
Chromis dispilus	Pomacentridae	All	Topographic complexity	0.83	Kingsford (1980)
Chromis dispilus	Pomacentridae	All	Current speed	0.73	Kingsford (1980)
Chromis dispilus	Pomacentridae	Juveniles	Topographic complexity	0.53	Kingsford (1980)
Chrysophrys auratus	Sparidae	Juveniles	Turf-algae cover	0.79	Kingett & Choat (1981)
Forsterygion varium	Tripterygiidae	Adults	Topographic complexity	0.82	Thompson (1979)
Notolabrus celidotus	Labridae	Juveniles	Shallow-Macroalgae cover	0.94	Jones (1984b)
Notolabrus celidotus	Labridae	Juveniles	Deep-Macroalgae cover	0.90	Jones (1984b)
Notolabrus celidotus	Labridae	Adults	Topographic complexity	0.59	Jones (1984c)
Parapercis colias	Parapercidae	Juveniles	Turf-algae cover	0.79	Mutch (1983)
Parapercis colias	Parapercidae	Adults	Macroalgae cover	-0.68	Jones (1981 a)
Parika scaber	Monacanthidae	Adults	Sessile-invertebrate cover	0.86	Jones unp. data
Pempheris adspersus	Pempheridae	All	Topographic complexity	0.89	MacDiarmid (1981)
Scorpis violaceus	Kyphosidae	Juveniles	Topographic complexity	0.81	MacDiarmid (1981)

Various studies have focussed on the variations in abundance and diversity of reef fish on temporal scales (Gosline, 1965; Golovanj, 1973), but most of these were in coral reef environments. However, habitats in temperate waters differ considerably from their tropical counterparts. Tropical environments consist mainly of large coral reef structures (Barnes & Hughes, 1982), whereas temperate reefs in New Zealand are characterised by stands of macroalgae with the major concentration of biomass found in less than eight metres depth (Choat and Schiel, 1982). There is, however, only limited information about fish assemblages in temperate waters of New Zealand and most of the work has been done along the north-east coast of the North Island (Jones, 1988).

Temporal variation in abundance and diversity of local populations of reef fish occurs on scales ranging from changes within a day to periods greater than ten years (Holbrook *et al.*, 1994). Differences in the variability of patterns of abundance and habitat association of reef fish through time have been attributed to a wide variety of causes (Table 2.2), incorporating species and population dynamics, as well as environmental variables.

Table 2.2 Temporal scales of variation in assemblages of fish.
Reproduced from Holbrook *et al.* (1994) Table 1

Scale	Mechanism(s)	Examples
Within day	Time of day	Bray, 1981
	Tide	Hobson, 1965
		Hobson & Chess, 1976
		Jones, 1983 a
		Kingsford & MacDiarmid, 1988
Within months	Lunar cycle	Ochi, 1989
		Thresher *et* al., 1989
Within years	Seasons	Carr, 1991a,b
	Habitat alteration	Mathews, 1990
		Schmitt and Holbrook, 1986
		Terry & Stephens, 1976
Among years	Environmental disturbances	Cowen, 1985
	Habitat alterations	Cowen & Bodkin, 1993
	Oceanographic events	Ebeling *et al.*, 1980
		Ebeling *et al.*, 1985
		Ebeling & Laur, 1988
		Love *et al.*, 1991
		Schmitt and Holbrook, 1990 a,b
		Stephens *at al.* 1984
		Stephens & Zerba, 1981
>10 years	Long-term environmental change	Choat *et al.*, 1988
	Oceanographic event	Ebeling *et al.*, 1990
		Stephens *at al.* 1986

The dynamics of local populations can also be influenced by recruitment processes (Doherty, 1980). Because pulses of newly recruited juveniles may vary annually in intensity, they are likely to produce irregular patterns of diversity and abundance. Holbrook *et al.* (1994) found that the black spot goatfish *Parupenus signatus* showed occasional peaks in abundance, resulting from strong recruitment years, which do not occur each year. They also stated that temporal variation in the diversity and abundance of reef fish can be caused by temporal variation in local habitats and other reef attributes.

Although reef habitats may exist for many years, changes can occur rapidly (Holbrook *et al.*, 1990). This rapid succession of states is believed to be one of the contributing factors influencing the dynamics of some temperate reef fish. Experimentally cleared areas of kelp forest showed a decrease in fish species' density (Bodkin, 1988). According to Ebling & Laur (1988), a change from barren flats to kelp forest is likely to result in a net increase in fish abundance and diversity.

Mechanisms operating over a relatively short term are usually related to behaviour of individuals, for instance feeding migration or movements related to spawning. These migrations appear to play an important role in the determination of diversity and abundance. Samoilys (1997) showed that in common coral trout, *Plectropomus leopardus*, movement patterns depended on fish size and season. Matthews (1990) found that rockfish, *Sebastes* spp., also show a seasonal component in distribution, caused by movement in response to habitat quality. Changes over longer time frames are typically caused by demographic processes. Different species in any given assemblage, however, may show contrasting patterns of behaviour or responses to demographic processes, and thus the degree of temporal variation (Holbrook *et al.*, 1994).

The aim of this chapter was to investigate and describe the abundance of reef fish around the Kaikoura Peninsula and their association with different habitats. It was anticipated that the distinct algal habitats found by Hickford and Schiel (1995) could be identified, in order to obtain comparable results. As stated in Hickford (1993), "ideally, these habitats and their associated environmental indicators could be used

to predict associated fish populations." In order to determine the mechanisms affecting the reef fish assemblages around the Kaikoura peninsula, depth was included into the experimental design. As a continuation of this work, associations between fish assemblages and reef habitats were examined through time.

2.2 Materials and Methods

2.2.1. Study sites

The abundance of common reef fish around the Kaikoura peninsula was assessed between December 1996 and December 1997. Prior to December 1996, several dives were carried out to identify potential habitats. Nine locations around the Kaikoura Peninsula were then chosen and marked with a buoy, in order to sample the same location each month (Plate 2.1). All sites were sampled once every month, with a minimum of three weeks between each count. Because reefs along the northeast coast of the South Island are more structurally complex and do not slope gradually, as they do in northern New Zealand (M°Cormick, 1989), it was difficult to sample three depths within one habitat. Therefore, sites in this study were not orthogonal to depth.

In December 1996 five 30 metre transects were used to determine the habitat structure. At five random points along the transect, the habitat structure, total seaweed cover and individual seaweed abundance within 4 m^2 were recorded. This was done for each of the nine sites. The characteristics of the nine sites are given in Figures 2.1a-i.

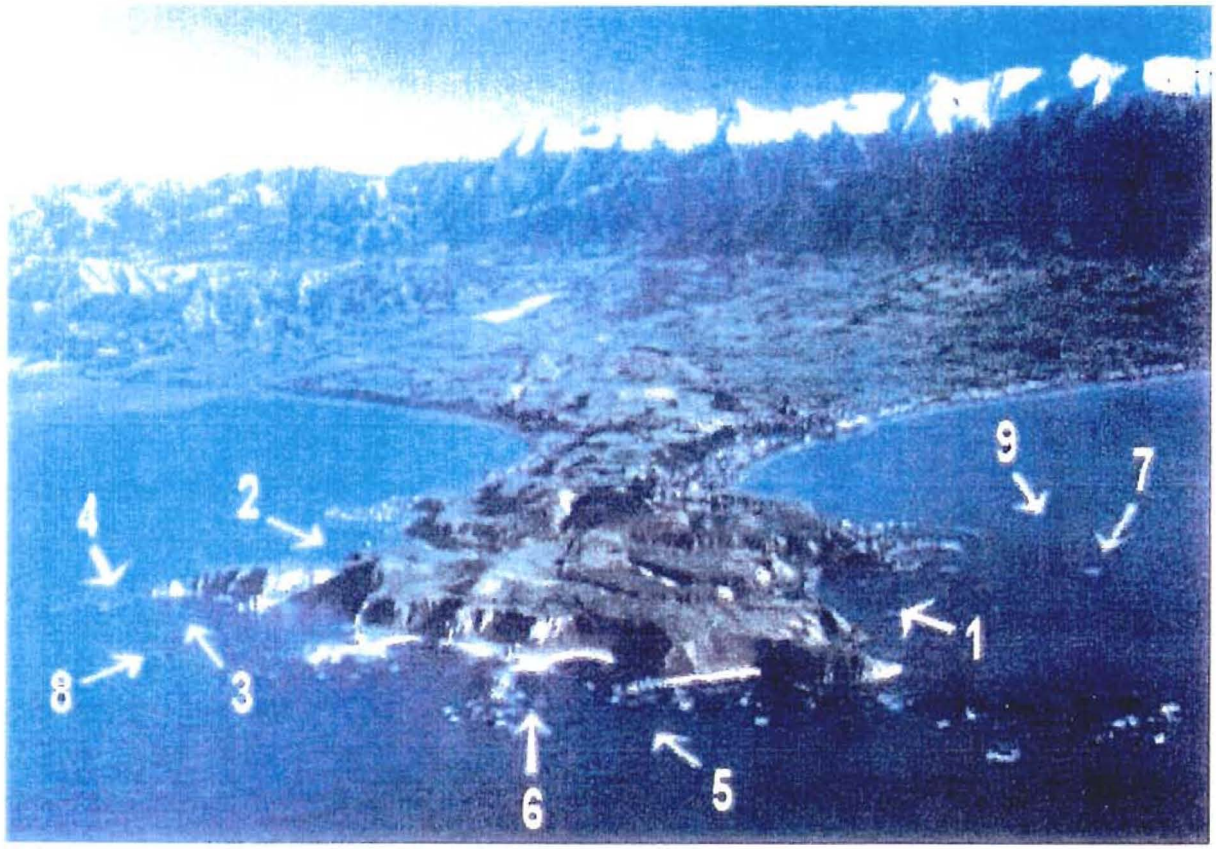


Plate 2.1 Aerial view of the Kaikoura Peninsula. Sites are marked with white arrows.

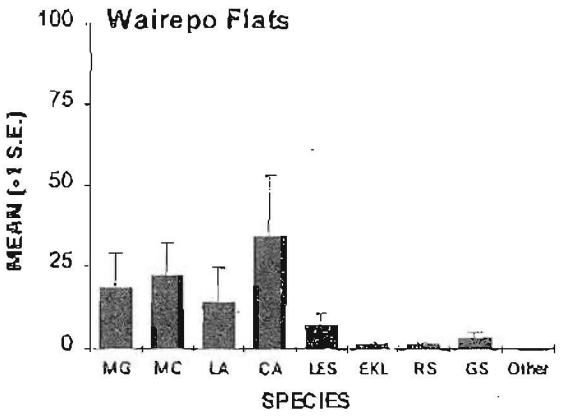
1. Wairepo Flats
2. Mudstone Bay
3. Whalers Bay
4. Sharks Tooth
5. First Bay
6. Spaniards Bay
7. St Kilda's Rock
8. Whalers Rock
9. Nine Pins

Shallow sites (0 - 6 m)

1. Wairepo Flats

Figure 2.1 a Mean % abundance of algal species at Wairepo Flats. For species codes see Appendix 1 A

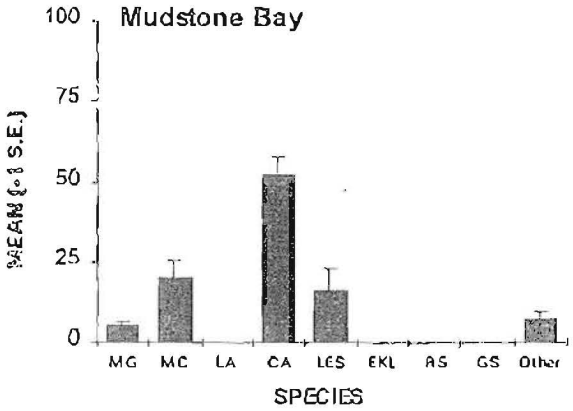
This site is characterised by medium sized boulders, rocks and crevices. Patches of sand and gravel are rare. Seaweed cover: 90-100%. Mixed seaweed composition, slight dominance of *Carpophyllum* (Figure 2.1 a).



2. Mudstone Bay

Figure 2.1 b Mean % abundance of algal species at Mudstone Bay. For species codes see Appendix 1 A

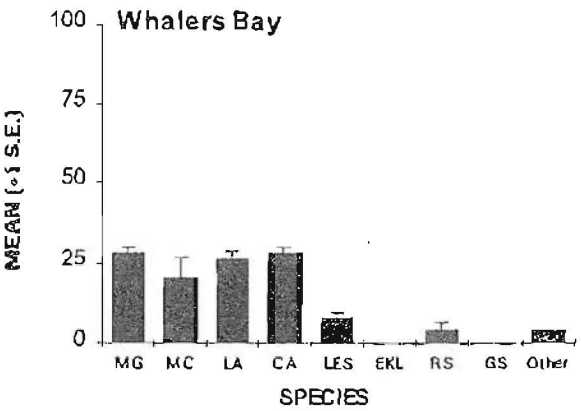
This site is characterised by large boulders, lying in close proximity to each other, thus creating deep crevices. Sand and gravel patches are found more frequently and are often covered by broken shells. Seaweed cover: 80-90%. *Carpo-phyllum* makes up >50 % of the algal composition (Figure 2.1 b).



3. Whalers Bay

Figure 2.1 c Mean % abundance of algal species at Whalers Bay. For species codes see Appendix 1 A

This site is characterised by small boulders and open areas of flat rocks, covered by dense algal carpets. Patches of sand and gravel are rare. Seaweed cover: 80-90%. Mixed seaweed composition of equal abundance of several species (Figure 2.1 c).

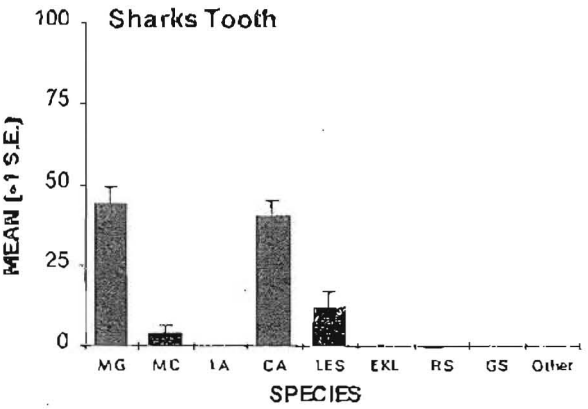


Intermediate sites (7 -11m)

4. Shark's Tooth

Figure 2.1 d Mean % abundance of algal species at Shark's Tooth. For species codes see Appendix One A

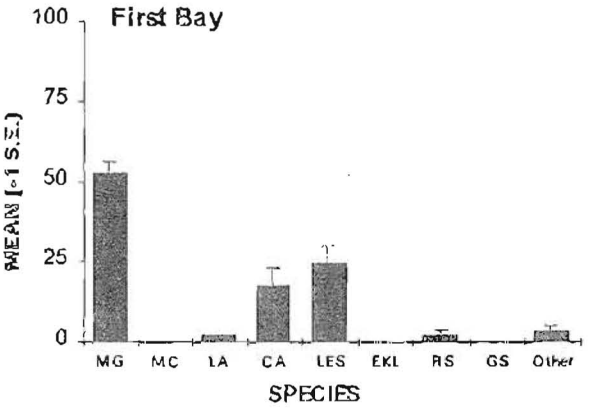
This site is characterised by smaller boulders and areas of flat bare rocks. Medium size cracks and crevices, seaweed abundance is patchy. Seaweed cover: 50-60%. *Marginariella* and *Carpophyllum* are the dominant species (Figure 2.1 d).



5. First Bay

Figure 2.1 e Mean % abundance of algal species at First Bay. For species codes see Appendix One A

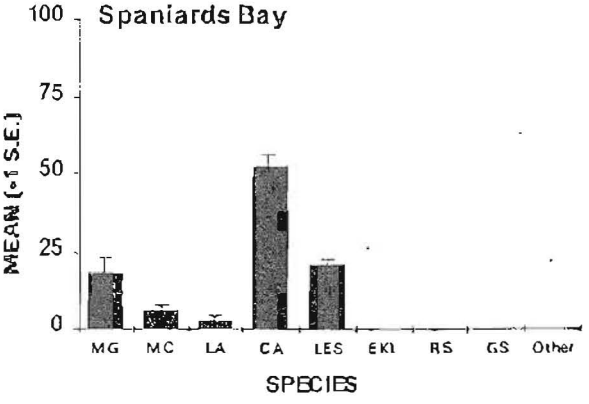
This site is dominated by medium and larger sized rocks. Areas of flat, algal-covered rocks are broken by sand patches. Seaweed cover: 50-60%. *Marginariella* is the dominant alga; *Carpophyllum* and *Lessonia* equally abundant (Figure 2.1 e).



6. Spaniards Bay

Figure 2.1 f Mean % abundance of algal species at Spaniards Bay. For species codes see Appendix One A

This habitat is characterised by the great abundance of large rocks and crevices. Small sand and cobble patches occur sporadically. Seaweed cover: 50-60%. *Carpophyllum* dominant species (>50 %), *Lessonia* and *Marginariella* equally abundant (Figure 2.1 f).

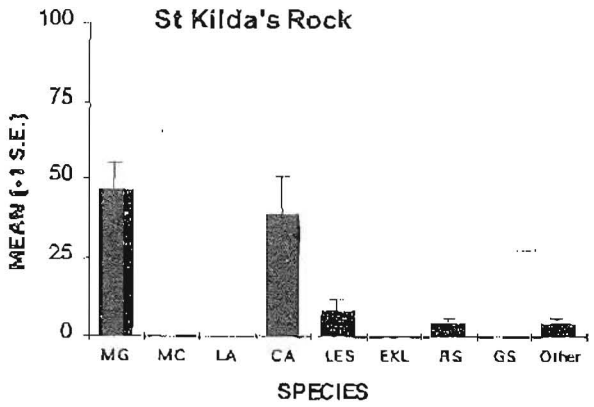


Deep sites (12 - 18 m)

7. St Kilda's Rock

Figure 2.1 g Mean % abundance of algal species at St Kilda's Rock. For species codes see Appendix One A

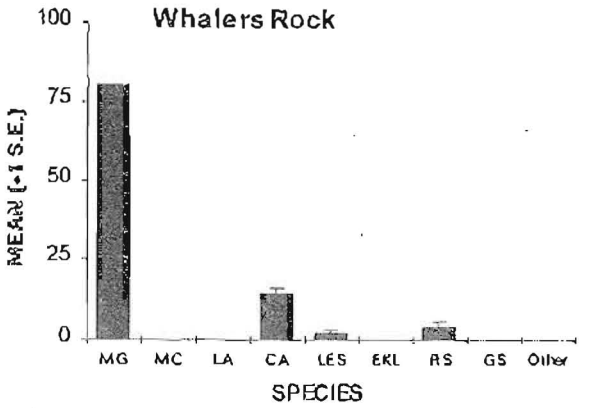
This habitat is dominated by patches of cobbled bottom with some small scattered patch reefs. Seaweed cover: 30-40%. Small patches of *Marginariella* and *Carpophyllum* (Figure 2.1 g).



8. Whalers Rock

Figure 2.1 h Mean % abundance of algal species Whalers Rock. For species codes see Appendix One A

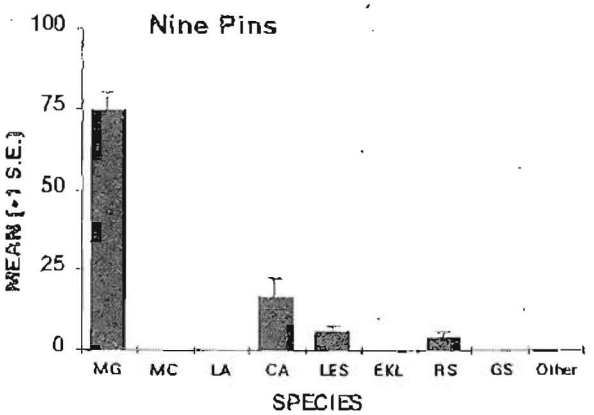
This habitat is characterised by large boulders and patches of sand and gravel. The rocks and boulders are mostly covered by coralline algae and small red algae. Seaweed cover: 20 - 25%. *Marginariella* most abundant (75 %); only small patches of *Carpophyllum* (Figure 2.1 h).



9. Nine Pins

Figure 2.1 i Mean % abundance of algal species at Nine Pins. For species codes see Appendix One A

This habitat is similar to St Kilda's Rock in that it is dominated by cobbled bottom, broken by small patch reefs. The rocks are either bare or covered by coralline algae and red seaweeds. Seaweed percentage: 20-30%. *Marginariella* most abundant (80 %), only small patches of *Carpophyllum* and *Lessonia* (Figure 2.1ib).



In order to include depth as a factor in the sampling design, the sites were grouped into shallow (1-6 m), intermediate (7-11 m) and deep sites (12-18 m). This resulted in a separation into three basic habitat types, according to specific physical and geological features, similar to those found in Hickford & Schiel (1995):

1. Shallow reef:

This area is characterised by medium rocks (< 1 m in diameter (D)) and areas of highly broken reef, creating lots of crevices. Patches of sand and gravel are rare and small. The total seaweed cover ranges from 70% to 100%, with a wide variety of algal species coexisting. The large brown algae *Carpophyllum maschalocarpum*, *Marginariella boryana*, *Macrocystis pyrifera*, *Cystophora spp.* and *Lessonia variegata* are dominant. Very small patches of exposed rock are covered by crustose coralline algae and patches of red algae. Yellowfoot paua, *Haliotis australis*, are often present, whereas blackfoot paua, *Haliotis iris*, are only seldomly seen. The depth ranges from one to six metres.

Sites: Wairepo Flats (1), Mudstone Bay (2), Whalers Bay (3)

2. Médium broken rock

This habitat is dominated by larger rocks (2 - 3 m D) and smaller boulders (5 - 6 m D). The total seaweed cover ranges from 50% to 70%. Crustose coralline algae are more abundant and there are some areas of bare space. The variety of seaweed is decreased, and the dominant algae are *M. boryana* and *C. maschalocarpum.* Some areas within this habitat are characterised by a layer of low-lying *M. boryana* and *L. variegata*, forming a thick algal carpet. The sea urchin *Evechinus chloroticus* is common in this habitat and usually occupies cracks and crevices, feeding on drift algae. There was a notable decrease in the abundance of the yellowfoot paua *H. australis* whereas blackfoot paua, *H. iris*, is more frequently found than in shallow areas. Sea tulips, *Pyura pachydermatina*, are also common. The depth ranges from seven to eleven metres.

Sites: Shark's Tooth (4), First Bay (5), Spaniards Bay (6)

3. Deep broken reef, cobbled bottom

This habitat is dominated by large rocks (3 - 4 m D) and boulders (> 10 m D), creating huge rock formations. Most rock surfaces are encrusted with coralline algae. The total seaweed cover is 20% to 40%, with *M. boryana* being the most common type. Sand and cobble patches have increased in size and frequency. The depth ranges from twelve to eighteen metres.

Sites: St Kilda's Rock (7), Outside Whalers Bay (8), Nine Pins (9)

2.2.2 Fish counts

Prior to the first counts in December 1996, exercises on identification and size estimation were done. Divers used models placed along a reef and practised estimating the size and species of fish (McCormick & Choat, 1987).

For the determination of fish abundance, the strip count method used in Hickford & Schiel (1995) was adopted. This method was shown to be the most accurate and precise within the constraints of time, effort and water clarity in the often murky conditions around Kaikoura (Hickford, 1993). All observations were done between 8 a.m. and noon. Five 30 x 5 metres transects (i.e., 2.5 m either side of the transect line), using a fibreglass tape, were placed randomly at each site, providing a mean estimate of density per 150 m^2. One diver laid out the transect, then returned to the starting point. Because some species, such as *N. fucicola* and *N. celidotus*, have been observed to follow divers (Jones, 1983 a), the divers then ascended 2-3 metres for three minutes before starting to count.

Fish were counted while swimming along the pre-laid tape at a constant speed. The divers maintained a position one metre above the substratum, keeping abreast of each other throughout the transect. During each transect, the number, size (standard length in mm) and sex (where visually identifiable) of all mobile reef fish seen within 2.5 metres of each side of the tape were recorded. In order to minimise the recording time (Sale & Sharp, 1983), the slates were pre-formatted with the names of the 12 most

common species. Small cryptic fish, such as blennies and triplefins, were excluded from the counts. To avoid double counting of individuals, fish crossing the tape were assumed to be already counted by the other diver. If a school of fish was seen within the transect area, the mean size and estimated total number of fish were recorded. After the fifth transect the water temperature was recorded. Because underwater visibility is known to be a critical factor influencing the accuracy of visual transects (Bortone *et al.*, 1986), transects were only done when visibility exceeded 2.5 metres.

The abundance of all mobile reef fish in the three habitats was described. Spatial and temporal changes in the four most common species were described and graphed. Analysis of variance (ANOVA) was done to test the effect of time and depth on the four most abundant species. Data were first tested for homogeneity using Cochran's C test and transformed (log (x+1)) if necessary. Some variances could not be stabilised. Analyses were done using Statistica (StatSoft Inc., release version 5.1).

2.3 Results

During the 585 transects twelve species and a total of 7144 fish were observed, including herbivores and carnivores (Figure 2.2).

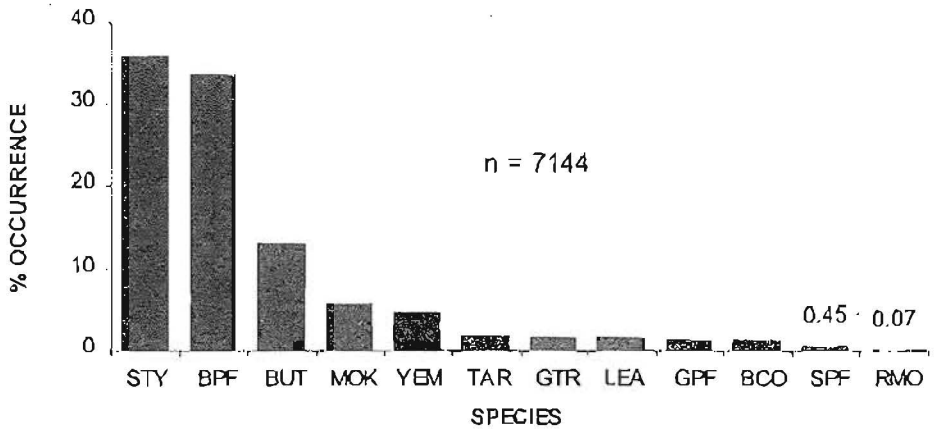


Figure 2.2 Percentage occurrence of species seen through time at all sites (n = total number of fish observed). For species codes see Appendix One A.

Spotties, *Notolabrus celidotus*, and banded wrasse, *Notolabrus fucicola*, were the most common species seen, comprising almost 70% of all species observed. Butterfish were the third most abundant species (13%), followed by blue moki, *Latridopis ciliaris* (5%). All remaining species were observed in considerably lower numbers.

The mean number of species and fish (Figure 2.3) recorded per transect (150 m^2) were relatively low and this was similar at all depths. During each transect, two to three species and 12 to 14 individuals were observed.

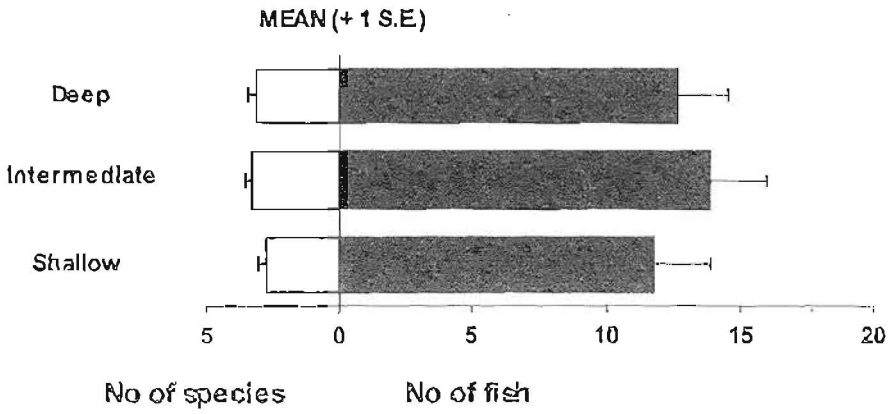


Figure 2.3 Mean number of species and individuals observed per transect at three different depths (all sites combined). (Number of transects within each depth = 195)

With the exception of yellow-eyed mullet, *Aldrichetta forsteri*, and leatherjackets, *Parika scaber*, infrequently observed species (< 5% of the total number of fish counted), were observed in similar numbers at all depths (Figure 2.4). *A. forsteri* showed greatest abundance within intermediate sites (7 - 11 m). *P. scaber* were found only in deep water habitats (12 - 18 m).

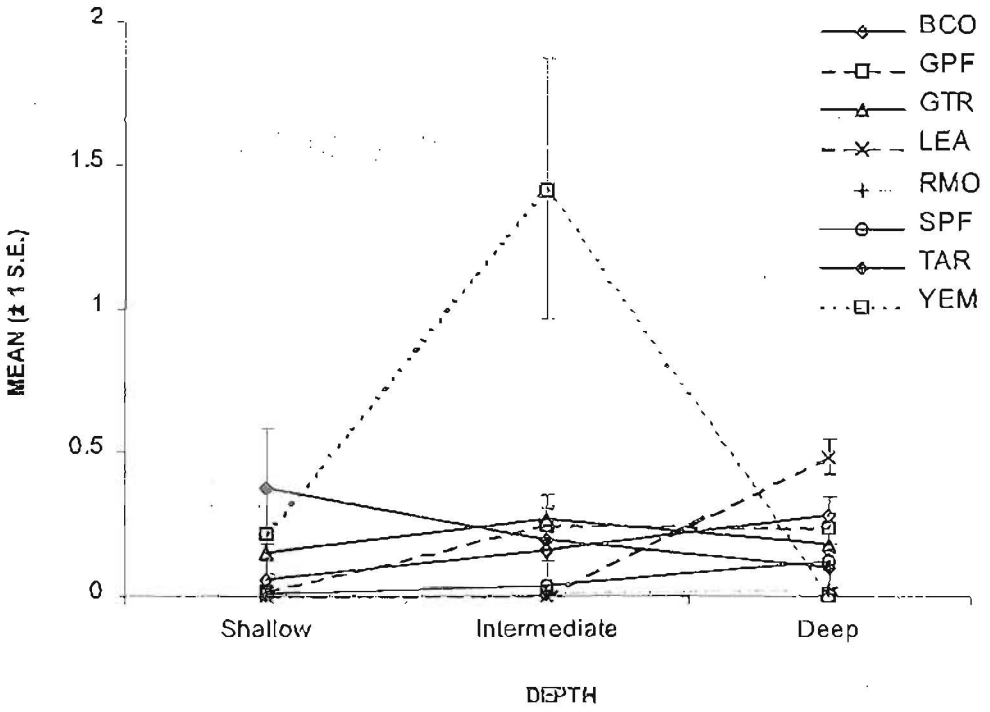


Figure 2.4 Mean number of species (occurrence < 5%) observed per transect at three different depths (all sites combined). Number of transects within each depth = 195. For species codes see Appendix One A.

2.3.1 Spatial variation

Species that accounted for < 5% of the total number observed were ignored in the following analysis. Analysis of variance showed significant differences in the abundance of the four most common fish, *N. celidotus*, *N. fucicola*, *O. pullus* and *L. ciliaris* among sites within depths (Table 2.3 - 2.6).

Table 2.3 Analysis of variance on the effects of time, depth and site (nested in depth) on the number of *Notolabrus fucicola*; sites treated as random factors. The data were initially transformed using log(x + 1) but remained heterogeneous.

Source of variation	df	MS	SS	F	p-level
time	12	0.34	4.08	2.69	0.0046
depth	2	2.16	4.32	1.34	0.3311
sites (depth)	6	1.62	9.72	31.38	0.0000
time x depth	24	0.25	6	1.67	0.0491
time x site (depth)	72	0.15	10.8	2.91	0.0000
residual	1086	2.022	2195.89		
total	1202				

Table 2.4 Analysis of variance on the effects of time, depth and site (nested in depth) on the number of *Notolabrus celidotus*; sites treated as random factors. The data were initially transformed using log(x + 1) but remained heterogeneous.

Source of variation	df	MS	SS	F	p-level
time	12	0.69	8.28	3.35	0.0006
depth	2	0.79	1.58	1.15	0.3775
sites (depth)	6	0.68	4.08	10.94	0.0000
time x depth	24	0.27	6.48	1.32	0.1806
time x site (depth)	72	0.21	15.12	3.31	0.0000
residual	1086	2.361	2564.05		
total	1202				

Table 2.5 Analysis of variance on the effects of time, depth and site (nested in depth) on the number of *Odax pullus*; sites treated as random factors. The data were initially transformed using log(x + 1) but remained heterogeneous.

Source of variation	df	MS	SS	F	p-level
time	12	0.69	8.28	3.35	0.0006
depth	2	0.79	1.58	1.15	0.3775
sites (depth)	6	0.68	4.08	10.94	0.0000
time x depth	24	0.27	6.48	1.32	0.1806
time x site (depth)	72	0.21	15.12	3.31	0.0000
residual	1086	2.361	2564.05		
total	1202				

Table 2.6 Analysis of variance on the effects of time, depth and site (nested in depth) on the number of *Latridopsis ciliaris*; sites treated as random factors. The data were initially transformed using log(x + 1) but remained heterogeneous.

Source of variation	df	MS	SS	F	p-level
time	12	0.18	2.16	2.69	0.0046
depth	2	0.17	0.34	3.98	0.0793
sites (depth)	6	0.42	2.52	1.14	0.3328
time x depth	24	0.61	14.64	0.87	0.6363
time x site (depth)	72	0.69	49.68	1.86	0.0000
residual	1086	0.25	271.5		
total	1202				

Within the shallow sites, more fish were observed per transect over all months at Whalers Bay ($\bar{x}$ = 17.7 ± 2.4) than in the other shallow sites ($\bar{x}$ = 8.8 ± 2.1). The high number of fish counted per transect in January was due to newly recruited spotties. Fish numbers observed at all shallow sites showed a gradual decrease towards the winter months reaching the lowest abundance in June and July, followed by a gradual increase with the onset of summer (Figure 2.5).

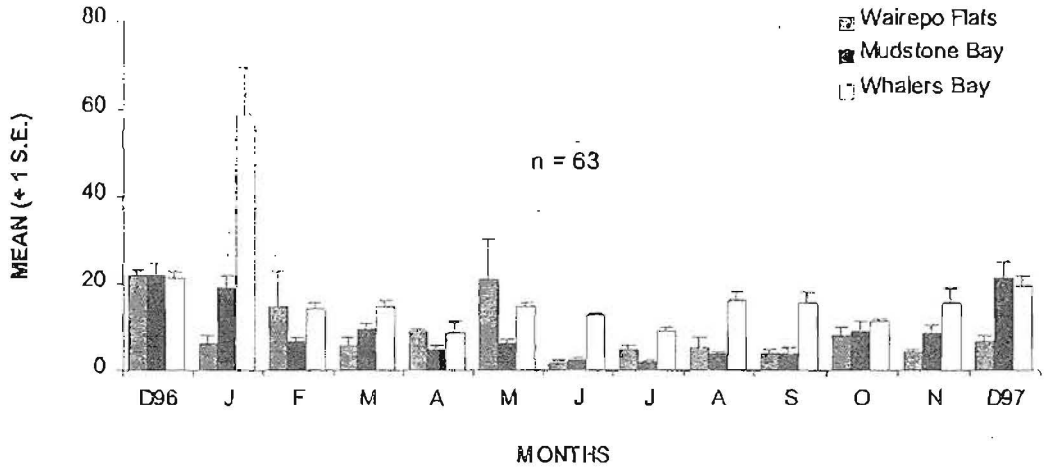


Figure 2.5 Mean number (+ 1 S.E.) of fish per transect at three shallow sites (0 - 6 m) (n = number of transects).

Sites at the intermediate depth appeared to show a gradual decrease in the mean number of fish per transect with the onset of winter, followed by an increase towards the following summer (Figure 2.6). However, Sharks Tooth showed a sudden increase in fish numbers in April, which was caused by the occurrence of the several large schools of yellow-eyed mullet. All three sites showed high abundances in January, which was due to newly recruited spotties and tarakihi. The high abundance of fish in June in Spaniards Bay can be largely attributed to the high but variable number of spotties and yellow-eyed mullets. The large number of individuals counted at Shark's Tooth and First Bay in October was caused by the occurrence of a large shoal of blue moki and several smaller shoals of yellow-eyed mullet.

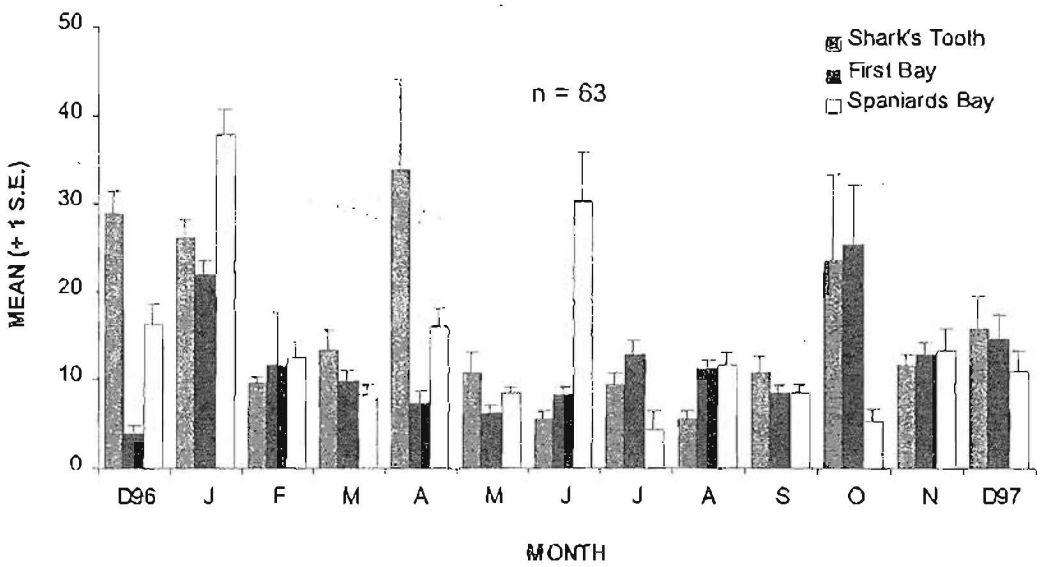


Figure 2.6 Mean number (+ 1 S.E.) of fish per transect at three intermediate sites (7 - 11 m) (n = number of transects).

Within the deep sites, fewer fish were observed at Nine Pins throughout the year than in any other site (Figure 2.7). St Kilda's Rock and Whalers Rock appeared to have similar abundances of fish between December 1996 and July but showed lower numbers between August and November. The high abundance of fish in February in St Kilda's Rock and Whalers Rock in December 1997 can be largely attributed to the high but variable number of spotties, banded wrasse and blue moki. The number of fish observed at Nine Pins gradually deceased to a low in October.

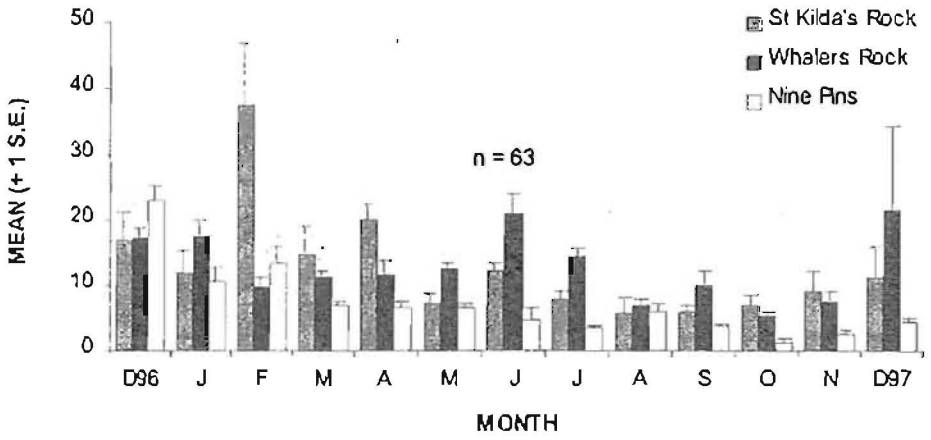


Figure 2.7 Mean number (+ 1 S.E.) of fish per transect at deep sites (12 - 18 m) (n = number of transects).

When all counts were grouped by depth, individual species showed differences in numbers between the three depths (Figure 2.8). Spotties were more abundant in shallow sites than in intermediate or deep sites. Banded wrasse were most abundant at intermediate depths. Butterfish were observed in similar numbers between all depths. Blue moki also showed similar numbers between the three depths.

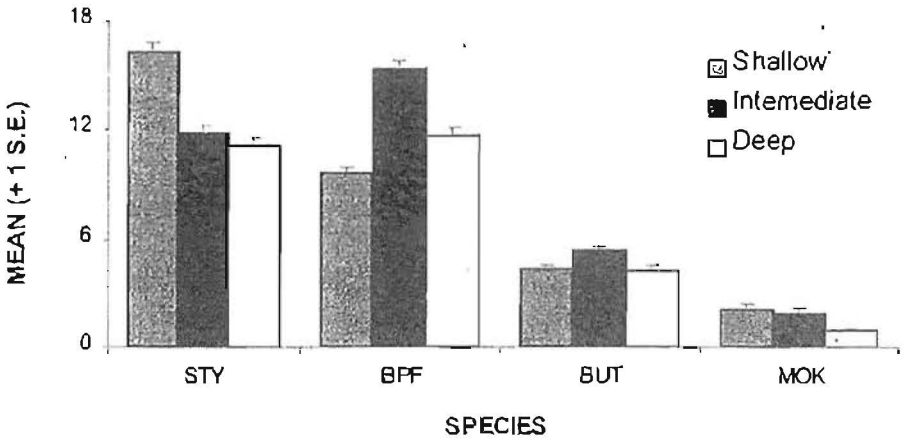


Figure 2.8 Mean number (+ 1 S.E.) of fish observed per transect at three depths. (number of transects per depth = 195), for species codes see Appendix One A.

2.3.2 Temporal variation

When all counts were grouped across depths and sites, overall temporal trends in fish abundance were more obvious (Figure 2.9). The four major species all showed a gradual decrease in numbers towards the winter. Numbers increased again with the onset of summer and similar numbers were observed for all species between December 1996 and December 1997. Blue moki was the least variable species.

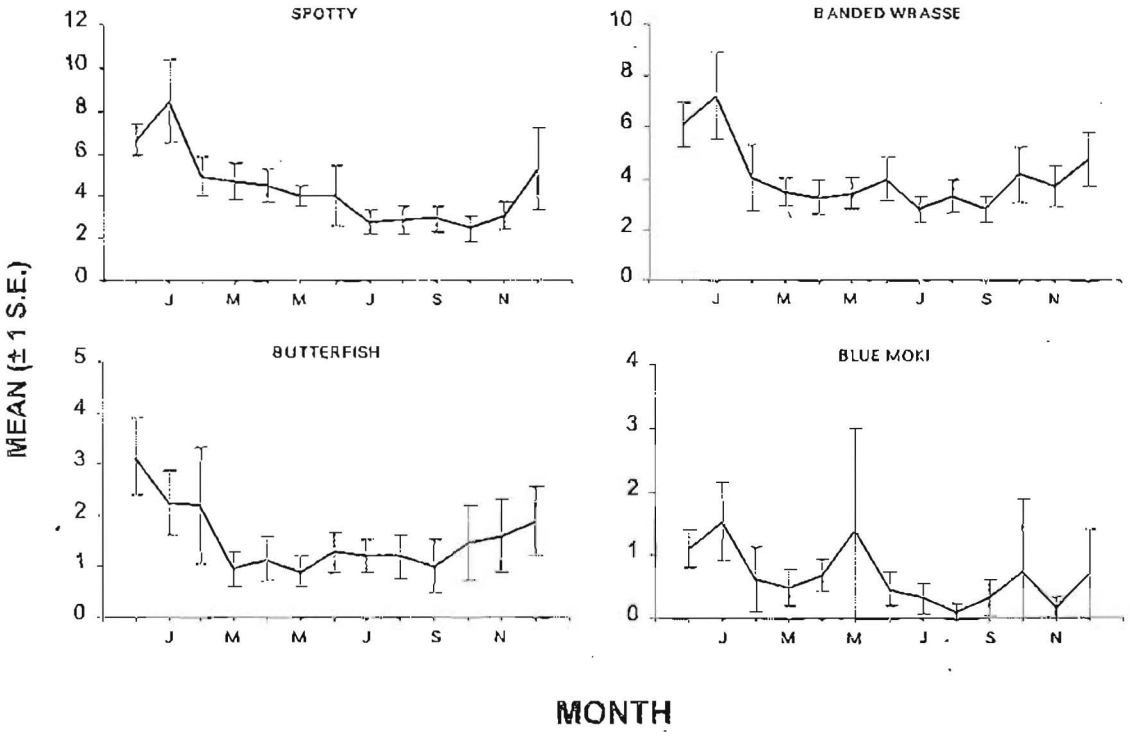


Figure 2.9 Mean number (± 1 S.E.) per transect of the four most common species of reef fish around the Kaikoura Peninsula (all sites combined). Note the different scales on the y-axes

As indicated in the ANOVA (Table 2.3 - 2.6), fish numbers varied among sites within depths (Figure 2.10). In the shallow sites (0 - 6 m), spotties were least abundant at Wairepo Flats. Banded wrasse and butterfish were most abundant at Whalers Bay and

blue moki were similar in numbers among the three shallow sites. At intermediate depths (7 - 11 m), banded wrasse, butterfish and blue moki did not differ much among the intermediate sites. Spotties, however, had reduced abundance at First Bay. In deep sites (12 - 18 m), three of the main species showed differences between areas. Spotties and banded wrasse were least abundant at Nine Pins, while butterfish were most abundant at St Kilda's Rock. Blue moki were never really abundant and were similar in numbers among sites.

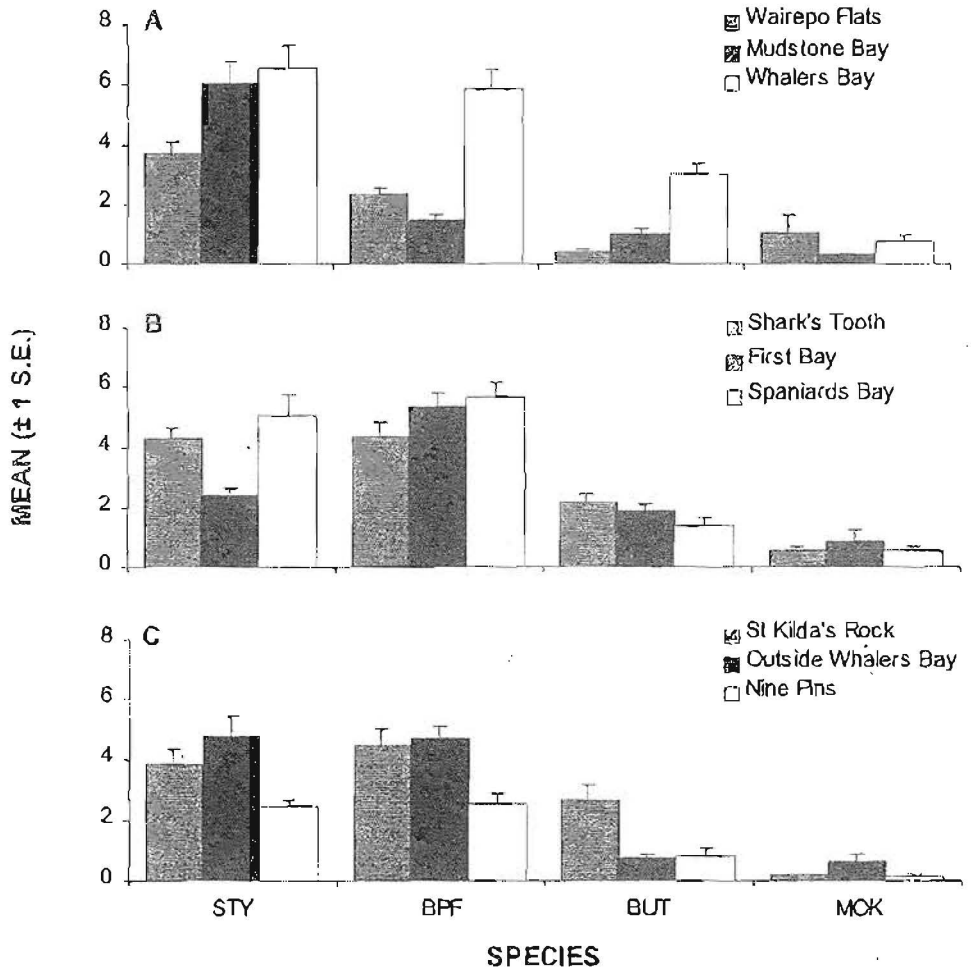


Figure 2.10 Mean number (+ 1 S.E.) per transect of the four most common species of reef fish (spotty, banded wrasse, butterfish, blue moki) at three different depths. A = Shallow; B = Intermediate; C = Deep. For species codes see Appendix One A

2.3.3 Butterfish abundance

Because butterfish are the focus of this study more detail is given about their abundance patterns. There was considerable variation in abundance through time of the three color stages (Figure 2.11). 'Juveniles' were dark yellow in colour with a distinct white lateral stripe. Those considered 'female' were brown-greenish coloured and those designated as males had a very dark, almost black colouration and had an elongated dorsal fin.

'Males' were the least variable through time and were usually the least abundant of the three stages. 'Females' were the second most abundant stage. They appeared to be more common in summer and were least abundant from March to May. 'Juveniles' were the most common stage throughout the year. The seasonal cycle was pronounced, the greatest numbers occurred in summer 1996, decreasing in winter and increasing again in the following summer (Figure 2.11).

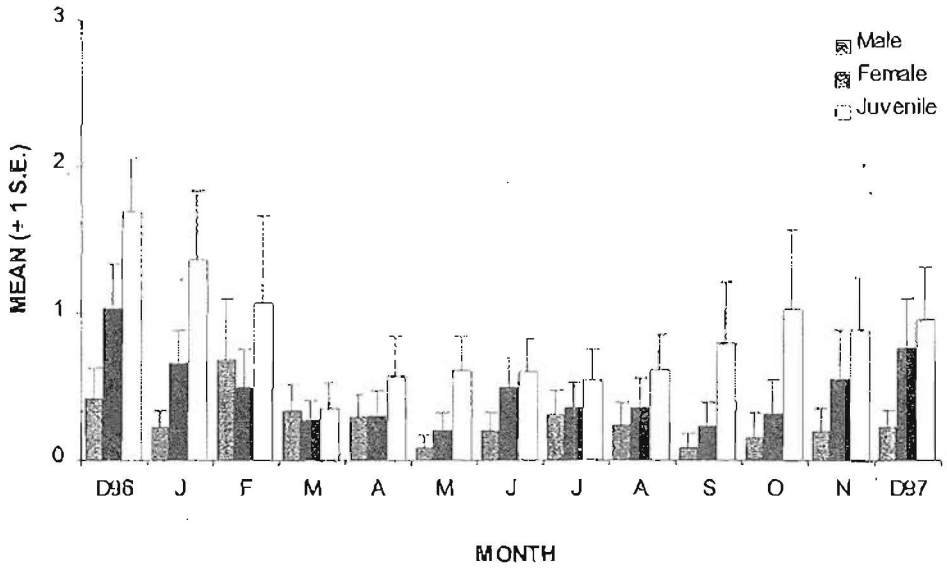


Figure 2.11 Mean number (+ 1 S.E.) per transect of 'male', 'female' and 'juvenile' *Odax pullus* around the Kaikoura Peninsula

When data for butterfish were pooled by depth, the number of individuals observed per transect appeared to vary between depths (Figure 2.12). 'Males' appeared to be more common within deep sites than in the shallow sites. 'Females' showed similar abundances at all three depths, while 'juveniles' were less abundant at deep sites.

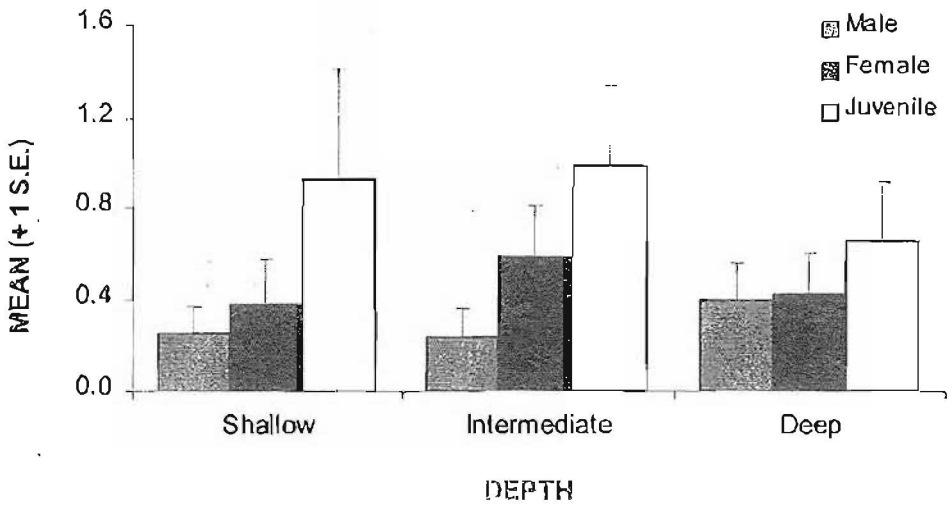


Figure 2.12 Mean number (+ 1 S.E.) per transect of 'male', 'female' and 'juvenile' *Odax pullus* at three different depths.

The average size of butterfish observed did not vary with depth ($F_{2,120} = 0.97$, $p = 0.381$).The size-frequency distribution of observed butterfish was similar between the three depths (Figure 2.13). The major mode in centimetre lengths was at 18 - 20 cm, with minor modes at around 6 cm and 25 cm. Shallow sites, however, tended to have more small fish (< 10 cm) than the other depths.

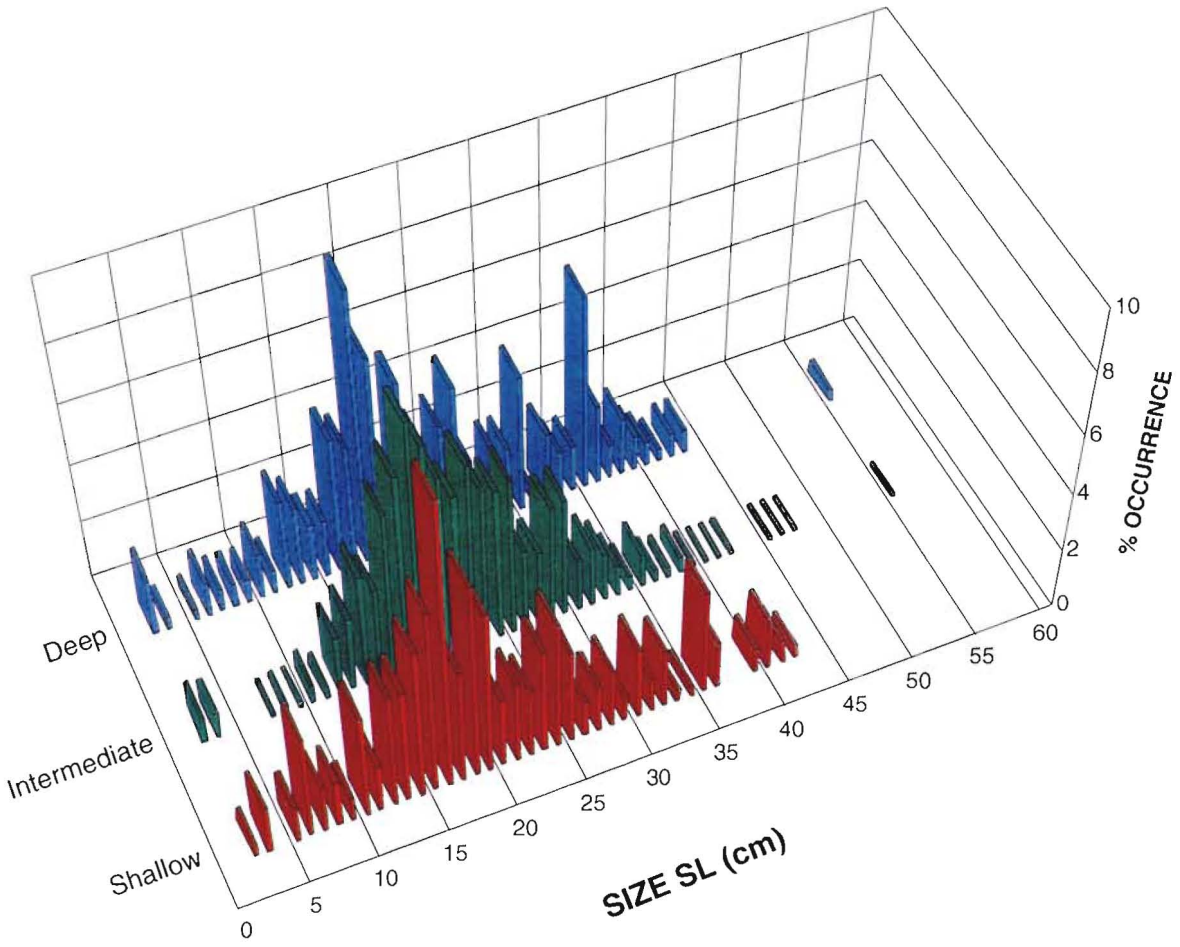


Figure 2.13 Size-frequency distribution of *O. pullus* at three different depths: shallow (n = 254), intermediate (n = 1035) and deep (n = 264). n = number of fish observed

2.4 Discussion

2.4.1 Habitat association

Recent literature has highlighted the close association of fish with specific topographic or biological characteristics of their environment. The rocky subtidal region around the Kaikoura Peninsula, however, is topographically and biologically complex. Factors such as depth, topography and presence/absence of certain fauna and flora, however, are often closely linked. The biological and physical differences between habitats in northern New Zealand and the eastern South Island appear to be reflected in the number of mobile reef fish species seen in transects. During this study, twelve species were seen and this number was supported by Hickford & Schiel (1995) who recorded eleven species in the same region. Studies done within the warmer waters of the North Island, however, found considerably more species, with Choat & Ayling (1987) recording 22 species of fish. Francis (1996) noted a linear decrease in diversity with increasing latitude which he ascribed to the influence of the major oceanic currents around New Zealand. While the northern fish fauna is under the influence of warm, subtropical currents (Heath, 1985), the diversity of reef fish around Kaikoura and other habitats in southern New Zealand is strongly influenced by the colder waters of the Southland Current (Heath, 1972).

Throughout the study period the species diversity of mobile reef fish across the three depths was generally low. Although a similar number of species was observed at each depth, considerably more individuals were seen in the sites at intermediate depth (7 - 11 m). Shallow waters generally supported smaller fish and larger fish were found generally in deeper waters. By definition, intermediate depths supported a broad mixture of both large and small fish. These fish are likely to enter this zone from the neighbouring shallow and deep waters. The intermediate depth zone also has the greatest habitat diversity, which could have contributed to the increased abundance of fish found there. This relationship was also found by Hickford & Schiel (1995), who found the greatest number of fish at sites with the most diverse habitat.

This study has shown that the four most abundant species around the Kaikoura Peninsula, *Notolabrus celidotus*, *Notolabrus fucicola*, *Odax pullus* and *Latridopsis ciliaris*, made up more than 87% of the resident fish fauna. *O. pullus* was the third most common species, comprising 13% of the total number of fish observed. Species of fish are not distributed randomly over the different habitats of a temperate reef environment. On a small spatial scale there appears to be distinct habitat segregation, with considerably different abundances of species found in areas ranging from 100% seaweed cover to flat coralline areas with only a few patches of macroalgae. The individual response of a species to the physical or biological characteristics of one habitat appeared to be an important factor in determining spatial patterns.

This study has found similar results to other studies, such as Kingett & Choat (1981), Choat & Ayling (1987), Holbrook *et al.* (1990) or Hickford (1993) investigating the spatial patterns of reef fishes. Around the Kaikoura Peninsula reef fish show a strong association with habitat type, which is mainly related to their feeding habits or the requirement for shelter. The most abundant reef fish, *N. celidotus*, was most common in all shallow sites. This corresponds to the positive correlation found by Jones (1984 a,b,c) between the abundance of spotties and macroalgal cover. He concluded that shallow areas with a high abundance of fucoid algae provided effective shelter and protection from piscivores, as well as harbouring a greater abundance of the preferred prey of spotties.

The second most abundant species, the large carnivore *N. fucicola*, was most common at all sites with intermediate depth. At that depth the habitat is very patchy with large areas of brown algae interspersed with smaller areas of coralline covered of bare space. The density of banded wrasse averaged around 4.1 individuals per 150 m^2. Banded wrasse are known to be selective feeders, with preferences for small hard shell invertebrates, such as crabs, limpets, small paua, mussels and small sea-urchins (Doak, 1991), which are found in intermediate depths. Kelp cover is still extensive in these depths and provides shelter and protection for adults and juveniles.

Another large carnivore, *Latridopsis ciliaris*, was found in similar numbers in habitats of all three depth zones. Choat & Ayling (1987) and Hickford & Schiel (1995) found

that blue moki were found in greatest numbers over sand or patch reefs. Blue moki search sandy and cobbled bottoms for small invertebrates. It was therefore believed that they would not tend to feed algal dominated habitats (Choat & Ayling, 1987). Adult moki are generally found over sandy bottom below 30 m, but juveniles < 30 cm long are believed to be found over reefs at all depths (Francis, 1988). The even distribution of blue moki in this study may be due to juveniles making up 82% of the total number of blue moki observed throughout the year and that each site contained at least a few small sand or gravel patches.

Habitats in southern New Zealand tend to be more diverse and less extensive than northern New Zealand. Subtidal habitats along the southeast coast do not have the extensive reef flats at 8 - 10 m, described for many sites in northern New Zealand (Schiel, 1988). Instead, the coralline-dominated flats in southern habitats tend to be patchy and dispersed among patches in intermediate depths. If there are fairly tight habitat associations of blue moki, it could be expected that they are spread across depths in southern New Zealand because the habitats also tend to be spread across depths, at least to 20 m.

The abundance of the butterfish did not vary with depth. This corresponds to the results shown by Meekan (1986). To some extent, these results are surprising because the abundance of butterfish has been positively correlated with macroalgal cover.Consequently, it was expected that the number of *O. pullus* would decrease in relation to the decrease in macrolagal abundance with increasing depth and, therefore, be more abundant in shallow waters. This was seen only at Whalers Bay, where more butterfish were found than at any other site.

M°Clanahan *et al.* (1994) and Jennings & Poulin (1997) showed that the abundance of a some species is affected by fishing pressure. There were few butterfish at Wairepo Flats and Mudstone Bay. Because of their sheltered nature and accessibility by boats, Wairepo Flats and Mudstone Bay are very popular fishing areas, with extensive recreational gill-net fishing and underwater hunting (Teirney *et al.*, 1992). Butterfish are one of the most frequently targeted species by recreational fishers along the east coast of the South Island and they are easily caught by gill-nets (Paul, 1997).

The minimum legal mesh size for gill-nets set specifically to catch butterfish is 108 mm. The minimum legal size is 350 mm fork length with a maximum of 30 fish per day (Amateur Fisheries Regulations, 1986). The regulations state that any person "shall, taking all reasonable care to ensure their survival, immediately return any finfish that is unlawfully taken or is of unlawful size back into the waters from which it was taken." However, once caught in a gill net, butterfish only survive for a very short time, sometimes less than one hour (pers. observation; Hickford, 1995). This results in them being removed from the population, even if undersized or in excess of the daily limit. Because a wide variety of mesh sizes (25 mm - 150 mm) are used by recreational fishers, this is likely to affect all size classes of the butterfish population.

Considerable differences were seen in the abundance of the three different colour stages of butterfish. Individuals with 'male' colouration showed the lowest abundance of all three stages, contributing only 16% of the total number of butterfish observed. 'Juvenile' *O. pullus* were very common, comprising more than 54% of all butterfish seen. Size specific changes in distribution are well-documented in marine fishes and may be attributed to different recruitment between habitats, availability of food due to dietary changes or vulnerability to predation (Helfman, 1978). 'Males' were more numerous in deep sites and were rarely seen at any other depth. Ritchie (1969) found similar patterns and concluded that male butterfish migrate into deeper water outside the breeding season.

The low abundance of males found at shallow sites within the reproductive season may have been a result of the patchy or clumped nature of adult distribution and diver-orientated behaviour (Meekan 1986). With increasing age, male butterfish tend to be more wary of divers. Once disturbed, large males usually flee from the source of disturbance rather than hide, unlike the juveniles and smaller females (pers. observation). It is therefore possible, that the disturbance of laying of the transect prior to the counts scared off some of the larger fish, thereby biassing the counts of males. 'Females' and 'juveniles' were observed in similar numbers at all depths. Their average size, however, increased with depth. This appears to be a common feature in species (Choat & Ayling, 1987, M^{c}Cormick, 1989; Kingsford *et al.*, 1989). For example, large specimens of the blue groper *Achoerodus viridis* showed greatest abundance within

deeper areas, while small and medium sized fish were more abundant in shallow and intermediate depths respectively (Gillanders, 1995).

2.4.2 Temporal variability

The relative abundance of fish within the assemblage varied among seasons. Species diversity, however, did not fluctuate greatly. Other studies have also shown that patterns of habitat associations are relatively stable trough time (Kingett & Choat, 1981; Jones, 1984; Holbrook *et al.*, 1994). Most species around Kaikoura followed a pattern of lowest numbers during winter and greater numbers in summer. The decrease in the relative abundance of fishes, however, was more substantial. The average number of fish counted during the winter months was less than a third of those seen during the summer.

Changes in diversity and abundance of reef fish can be attributed to many causes, including the dynamics and characteristics of the reef and the fish themselves (Holbrook *et al.*, 1994). It has often been suggested that colder temperatures could influence the activity patterns of reef fishes (Stephens *et al.*, 1984; Helfman *et al.*, 1997). During colder months, individuals may show decreased feeding activity and may spend more time resting and hiding among the weed. For example, Deady & Fives (1995) showed that the corkwing wrasse *Crenilabrus melops* fed considerably less during the colder winter months. Less active fish by definition are less likely to be counted in visual transects. Therefore, the observed decrease in abundance of some species during winter may have been the result of varying activity patterns.

Variation in the total abundance of all fish species between seasons also appeared to be the result of generally strong seasonal recruitment patterns in some species (e.g. *N. celidotus* and *N. macropterus*). Changes in species diversity appeared to be partly caused by the seasonal abundance of newly recruited individuals from other species. For example, only the juvenile stages of tarakihi, *Nemadactylus macropterus*, were

seen, but only between December and March. Adult tarakihi usually occur at depths of 50 to 200 m and are unlikely to be encountered in visual transects. Juveniles, however, are concentrated in nursery areas within shallow and intermediate depths, gradually migrating into deeper water with increasing size (Francis, 1988).

Other migratory movements may also have contributed to the lower abundance of fish observed during the winter months. The abundance of blue cod, *Parapercis colias*, seemed to be influenced by general migrations. Tagging experiments have shown that large adult cod (40 - 60 cm) move only short distances whereas younger individuals move up to 40 km (Francis, 1988). Because no cod < 40 cm was seen, it is likely that many *P. colias* could undergo migrations from site to site throughout the year.

Migration induced by spawning events may have also contributed to the lower number of fish counted during winter. Red moki, *Cheilodactylus spectabilis,* was seen only during the summer. Throughout the year, this species exhibits a spatial separation of sexes, with adult females occurring in groups in areas shallower than 15 m and males inhabiting deeper waters, usually below 20 m. During the spawning season, however, females migrate into deeper waters. Jones (1984 a,b) showed that even though there is no spatial separation of the sexual stages in spotties recognisable, adults tend to move into deeper waters during the spawning season in late winter.

Small scale, seasonal movements, influenced by changes in temperature and climate can affect the diversity and abundance of species in particular habitats. Migration caused by changes in temperature was first noted in labrids for the cuckoo wrasse *Labrus ossifagus* (Lönnberg & Gustafson, 1936). During the warmer months *L. ossifagus* inhabit shallow waters, but migrate towards deeper habitats with decreasing temperatures. Similar seasonal movements have been observed in *Xyrichthys novacula* (Terao *et al.*, 1991). Helfman *et al.* (1997) stated that many reef fish leave shallow water habitats when algae die off during winter. Graham (1956) noted that *Notolabrus fucicola*, *N. celidotus* and *Pseudolabrus miles* exhibited very low abundances during the winter in Otago Harbour.

The increased abundance of individuals at the end of the summer may have been related to increased activity caused by the end of the spawning season. Some species may increase their feeding activity to compensate for the increased energy requirements during the reproductive months (Ware, 1984).
Oceanographic events might also have been a determining factor in the decrease of individuals during the winter. Increased mortality and reduced growth have been noted in Pacific salmon populations off Oregon and Washington after El Niño events (Thayer & Barber, 1994). The effects of El Niño are known to affect the weather patterns in New Zealand (Anon., 1994). Around the Kaikoura Peninsula there was a high mortality of shellfish and other invertebrates, including sea urchins, *Echinus chloroticus*, yellowfoot paua, *Haliotis australis*, and crayfish, *Jasus edwardsii*. Other smaller invertebrates may also have been affected, which in turn may have affected the reef fish populations by reducing the amount of prey available.

2.4.3 Size differences

There were no differences in the sizes of *O. pullus* among depths. This is in contrast to other studies that have found increasing fish size with increasing depth for many fish species (e.g. Ritchie, 1969; McCormick, 1989; Gillanders 1995 b). The similarity in the sizes of observed *O. pullus* may have been caused by the similar habitats found at all depths. Subtidal habitats around Kaikoura do not exhibit the distinctive changes from algal dominance to bare flats with increasing depth, found in the North Island. Although the overall cover of macroalgae decreases in deeper waters, they can be found at all depths to 20 m around Kaikoura. This may provide the necessary shelter to enable spawning in deeper sites. Meekan (1986) showed that *O. pullus* in the North Island recruit exclusively into algal stands within shallow waters. However, within this study, newly recruited butterfish (< 4 cm) were seen in depths to 18 metres. Therefore, recruitment around the Kaikoura Peninsula is probably not restricted to shallow waters.

Ayling (1978) concluded that the six habitats described in his study in north-eastern New Zealand represented meaningful biological divisions. Around Kaikoura there were considerable differences in the abundance of some species between sites at similar depths. Demographic studies of particular species will undoubtedly help explain the finer scale variations in fish abundances, as has been the case elsewhere (Jones, 1984 b,c). The incorporation of habitats, depths and sizes are a good framework for understanding variation in reef fish diversity and abundance along the north-eastern coast of the South Island.

CHAPTER THREE

Reproduction and Age Determination

3.1 Introduction

Temperate marine teleost fishes show a wide range of life-history traits. Numerous studies have investigated the reproductive strategies, sex change patterns and social system in tropical labroid fish (Robertson, 1972; Robertson & Choat, 1974; Roede, 1972; Warner, 1975; Robertson & Warner, 1978). The social systems of these fish are often closely related to their complex life history (Tribble, 1982). Studies comparing the functional morphology of the Labridae, Scaridae and Odacidae have shown that these families form a monophyletic assemblage of pharynognathous acanthopterygian teleosts (Liem & Greenwood, 1981). Considering this close relationship, it is likely that these families exhibit similarities in their life history and reproductive strategies (Crabb, 1993).

3.1.1 Reproductive seasonality

Most marine teleosts have a seasonal reproductive cycle with eggs and larvae being produced when environmental conditions are the most conducive for offspring survival (Bye, 1984). This is likely to be during times of increased zooplankton production during spring and summer (Jillet, 1971). Distinct reproductive cycles are a very common feature in many fish species but are often more pronounced in species inhabiting waters at temperate latitudes (De Vlaming *et al.*, 1982). These cycles are controlled by endogenous rhythms which correspond to environmental conditions (Bye, 1984) and are reflected in the seasonal variations of gonad weight and size. Each individual stage of the reproductive cycle is associated with changes in abiotic factors, such as photoperiod, currents, lunar cycles or sea temperatures (Whittier & Crews, 1987).

Sea temperatures are likely to influence reproductive timing of most temperate reef species. In contrast to many tropical reef fish, which spawn year-round, the majority

of temperate reef fish species spawn only within the warmer months of spring and summer (Jones, 1988; Kingsford, 1988, Ebeling & Hixon, 1991). The reproductive season of *Odax pullus* is believed to be up to 10 months long (Ritchie, 1969) although there appear to be latitudinal differences in the start of the spawning season, its duration and the peak spawning times.

The reproductive season of *O. pullus* populations within Cook Strait extends from July to March and peak spawning is believed to occur between September and October, based on gonad condition and by the presence of eggs in the plankton (Ritchie, 1969). Like most other coastal reef fish, *O. pullus* have planktonic eggs, thus their dispersal is closely related to nearshore currents (Doherty *et al.*, 1985). Robertson (1973) found butterfish eggs only from October to January and suggested that the spawning season in the colder water of the South Island was shorter than in northern regions. This was supported by Crabb (1993), who described the spawning season in Otago as extending from October to January.

During their spawning season, butterfish function as a partial spawner. Ritchie (1969) found that most fish caught between July and February contained ripe gonads, while completely spent ovaries were rare. In addition, recently fertilised ova were found in plankton samples throughout those eight months. Partial spawners show multiple spawning events, rather than a single spawning where all the ova are released at once. Extended partial spawning seems to be a good adaptation to ensure maximum survival of spawn in coastal rocky environments subject to frequent storm events (Doak, 1972).

Temperate reef species commonly show complex reproductive strategies and are usually very selective in spawning sites and times. Spawning migrations into deeper water are commonly found in labrids and cheilodactylids. This is believed to minimise egg predation (Warner *et al.*, 1975; Johannes, 1978). Selectiveness of spawning sites may enable reef fish to maximise offspring dispersal and survival (Barlow, 1981;

Doherty *et al.*, 1985). Jones (1981 b) showed that in spotties, *Notolabrus celidotus*, the spawning rate increased exponentially with increasing depth of the territory. Jones & Thompson (1980) showed that spotties also exhibited increased spawning activity very early in their reproductive season. This may be beneficial to offspring survival because of the increased production of zooplankton. Cunner, *Tautogolabrus adspersus*, also show greatest spawning activity early in the spawning season (Pottle & Green, 1979). However, Jones & Thompson (1980) pointed out that benefits of early spawning for offspring survival have not been demonstrated.

3.1.2 Protogynous sex change

Sex change is very common in teleost fishes (Charnow, 1982) and was first described in the green swordtail, *Xiphophorus helleri* (Essenberg, 1926). A species is considered to be hermaphroditic if a significant proportion of individuals in the population function as both sexes (Sadovy & Shapiro, 1987). However, hermaphroditism only describes species and not individuals. Hermaphrodites may be synchronous (simultaneous) when both eggs and sperm mature at the same time, or asynchronous (consecutive) when a fish functions as either male of female at any one time (Potts & Wootton, 1984). Male and female tissue, when present, must be functional and the occurrence of individuals functioning as both sexes must be relatively widespread throughout the population (Sadovy & Shapiro, 1987).

To describe the life history of a species in a population, three types of hermaphroditism have to be differentiated: simultaneous hermaphroditism, protogyny and protandry. Simultaneous hermaphrodites possess functional ovaries and testes at the same time. Protogyny describes a change from a functional female to a functional male (e.g. Choat & Robertson, 1975; Jones, 1980; Koulish & Kramer, 1989), whereas protandry describes a male-to-female change (e.g., Warner, 1984; Calvo *et al.*, 1992). The succession from one sex can be defined as the "change from the

possession of recognisable ovarian tissue to that of testicular tissue, and vice versa" (Atz, 1964).

According to Storch & Welsch (1991) there are at least four families within the order of Perciformes for which simultaneous hermaphroditism (Serranidae), protandry (Sparidae) or protogyny (Serranidae, Sparidae, Centracanthidae, Labridae) is present. Reinboth (1962) reported the existence of Protogyny in several species of labrids, and more recent investigations have shown that protogynous hermaphroditism is the most common reproductive pattern in the Labridae (Gillanders, 1995 a). In protogynous labrids, males either develop directly from the juvenile stage or by sex reversal from adult females (Dipper & Pullin, 1979; Sadovy & Shapiro, 1987). A species is considered monandric if only secondary males are present which have developed from sex reversal, or diandric if primary and secondary males occur in the species.

The rapidity of sex change appears to be adaptive. A dominant female can change sex only if she is able to defend her new territory against competing males (Crabb, 1993). Therefore sex reversal is usually a very rapid process, especially in many tropical species (Robertson, 1972). Sex change in most temperate fish is seasonal, whereas in some tropical reef fish it can occur throughout the year (Ross, 1984). For example, the saddleback wrasse *Thalassoma duperrey*, lives in sexually integrated home ranges and mating appears promiscuous rather than in harems. Within this species, sex change does not occur to replace dominant males but is a function of size and number of conspecifics in the social group (Ross & Losey, 1983).

The mechanisms and reasons for sex reversal in fish have received considerable attention. The phenomenon of sex change requires both physiological and ecological explanations to be understood (Adkins-Regan, 1987). According to Ross (1990), sex reversal can be regarded as an adaptive mechanism within a social group, which is strongly influenced by ecological factors. One model frequently used to explain possible ecological determinants incorporates the size-advantage hypothesis which

is believed to be the only explanation for many instances of sequential hermaphroditism (Gishelin, 1969).

Adkins-Regan (1987) stated that "according to the size-advantage models, the relationship between reproductive success and size differs for the two sexes in such a way that the greatest lifetime reproductive success is achieved by reproducing as one sex at small size (young ones) and the other sex at larger sizes (older ones)". Hermaphroditism, therefore, would occur when the reproductive outcome of the opposite sex exceeds the success of the current sex. This suggests that sex reversal is genetically pre-determined and triggered by physiological events closely related to body size. Supporting evidence can be found in the size-sex separation of many protogynous species in which the females are generally small and males are larger (Jones, 1980; Shapiro, 1981; Nemtzov, 1985; Crabb, 1993).

Although sex reversal appears beneficial to the population by replacing the dominant individual with a fish of high fitness it may also have possible costs. Hoffman *et al.* (1985) showed that the Mexican and Spanish hogfish (*Bodianus diplotaenia* and *B. rufus*) showed periods of decreased mating success after sex change. This may be due to delays in the establishment of territories, resulting in a lower number of mating events (Gross, 1991). The physiological changes during sex reversal and increased energy requirements to convert reproductive cells and colour pigments may lead to slower growth.

There have been no definitive studies done on sex change in *O. pullus*, and the mechanisms that trigger sex reversal in butterfish are still unknown (Crabb, 1993). Ritchie (1969) and Paul (1997) suggested that at around 40 cm about half of the female butterfish transform into males. Graham (1956) noted the occurrence of a 3 : 1 ratio of female to male butterfish and suggested this was caused by protogynous sex change in this species. So far, no study has shown the occurrence of small males in *O. pullus* populations. Ritchie (1969) and Crabb (1993) both captured only males >

40 cm. This suggests that butterfish is a monandric species with males only developing from sex reversal.

3.1.3 Colouration

Most labroid species display a wide range of colour patterns during their development. Colour is an important indicator of social status and reproductive state. Within monochromatic species, females usually develop similar colour patterns to the males, whereas in dichromatic species each sex shows different colouration and patterns (Warner & Robertson, 1978). Butterfish colouration is mostly associated with ontogenetic stages (Ritchie, 1969, Chapter 1), but may also be associated with specific populations and diets (Russell, 1983; Meekan, 1986). Because there may be latitudinal variations in colour patterns, there is still confusion about the association of colour with sex and whether *O. pullus* can be classified as mono- or dichromatic (Ritchie, 1969, 1975, 1976; Doak, 1991; Crabb, 1993).

3.1.4 Ageing

Information describing population dynamics of most fishes is limited (Radtke, 1997). This especially pertains to age, growth, migration patterns, mortality, and longevity. Much of the important information detailing these parameters is based on age-dependent and environmental factors. This information is needed to describe demographic characteristics unique to specific life history events, as well as for an understanding of the growth and longevity of a species. In addition, the importance of ageing fish accurately is a prelude to management of stocks, particularly exploitation rates (Pitcher, 1993).

Age and size relationships of *O. pullus* are mentioned in the literature, mostly in accounts of sex change and reproduction. However, no definitive studies have been published and there is still debate about actual growth rates, maximum age and age at maturity. Ritchie (1969) was the first to describe the age and growth in butterfish. He used scale annuli to develop a back-calculated growth curve to age nine, with successive mean lengths-at-age of about 8, 15, 24, 32, 38, 43, 46, 48 and 50 cm (Paul, 1997). His study was limited, however, by the small number of young specimens. Crabb (1993) and Paul (1997) also determined the age in mature fish but both studies were limited by a very small sample size (21 and 7 fish respectively).

There are three basic approaches to age determination. The empirical approach uses data based on direct observation of individual fish held in confinement or of marked and recaptured fish (e.g., Beamish *et al.*, 1983). The age or time at large is known, thus this approach is more relevant as a means of age validation. The statistical method uses data based on the analysis of length-frequency distribution (see Hilborn & Walters, 1992 for review). This approach can be used to estimate age composition or mortality rates, but does not provide sufficient information specific to an individual (Hightower, 1996). The anatomical approach is based on the examination of calcified structures such as scales or bones.

Determining the age of fish using the anatomical approach has been an important tool in fishery management since Heinke (1898) found scales to be good age indicators (Sinclair, 1988). In recent years, the study of the relationship between growth and age in fishes has exerted an even greater role in investigations (Pitcher, 1993), and age determination, using calcified hard parts (osseochronometry), has been extensively applied in fisheries science (Weatherly and Gill, 1987). For a population that is only lightly exploited, the maximum age gives an indication of the fishing pressure that the population can withstand. Long-lived species, such as the sablefish, *Anoplopoma fimbria* (maximum age 100+) or the orange roughy, *Hoplostethus atlanticus*, (maximum age 130+), must be managed carefully to avoid overexploitation (Hightower, 1996).

Knowing the age and longevity of fish also extends the understanding of the dynamics of fish stocks and the reaction of fish populations to environmental stresses, natural mortality and predation.

3.1.4.1 Ageing structures and methods

Growth increments are evident within the hard parts of many plants and animals (Neville, 1967). In fish, calcified structures such as vertebral bones, scales and otoliths, exhibit these growth increment sequences in the form of rings. The shift from narrow to wider spacing is called an annulus, which is similar to marks on cross sections of tree trunks. Under transmitted light, these rings appear as opaque and translucent bands progressing outward from the centre (Buckley & Blankenship, 1990). In most fish species that have been examined, these bands are formed every year. Most temperate species, therefore, are believed to have increments that correspond to the age of the fish in years (Casselman *et al.*, 1987; Das, 1994). Furthermore, an indication of fast or slow growth periods is provided by the width of the calcium deposits.

Several studies have examined vertebrae and spines using electron microprobe and atomic analyses (Radtke & Caillet, 1984; Caillet & Radtke, 1987). Skeleton growth is usually an irreversible process, with rearrangement of minerals or bone reabsorption seldomly taking place (Simkiss, 1974). Similar to other structures, seasonal environmental factors influence the incorporation of elements into the skeleton (Casselman, 1982). Quantitative variation in the deposition of calcified tissues is not easily discernible, but microanalysis of elemental compositions may be possible. Jones & Geen (1977), for example, showed the possibility of measuring the concentrations of elements such as phosphorus and calcium, which are deposited in relation to seasonal growth rates and can be detected using X-ray spectrometry.

Within scales, ages are determined by interpreting patterns in the circuli. Age estimation is based on three assumptions. First, scales increase in size rather than in number with increasing length of the fish. Second, growth of scales is proportional to fish growth, and third, annual marks are formed at the same time every year (Jearld, 1983; Hightower, 1996). Otoliths can be used in osseochronometry because of seasonal differences in the concentration of organic matter that produces light and dark bands (Williams & Bedford, 1974). Rings on otoliths (annuli) are more widely spaced during peak growth and narrower in winter when growth slows. It is assumed that most fish produce these rings at approximately the same time every year. In teleost fishes, the otoliths are part of the vestibular apparatus and reside in the cranial cavity (Jobling, 1995). Three otoliths (sagitta, lapillus and asteriscus) can be found in the endolymphatic sac of the inner ear on each side of the brain (Lowenstamm, 1971). They are hard structures composed of calcium protein and are formed by the process of biomineralisation and function as sound receptors and for balance and orientation.

The annuli in scales can be unreliable for ageing fish because they can be reabsorbed during periods of starvation and stress (Mugiya & Watabe, 1977). Otoliths are not susceptible to reabsorption (Mugiya & Watabe, 1977; Campana & Neilson, 1985) and seem to remain unchanged once formed (Campana, 1983). For this reason, using increments found in otoliths is usually the most accurate and precise method to estimate the age of fish (Six & Horton 1977; Radtke, 1997).

3.1.4.2 Ageing error

Beamish and McFarlane (1987) caution that osseochronometry should not be applied to all fish species because some slow growing species do not produce annual increments. In addition, in some fish, the reliability of using scales for ageing decreases as linear growth diminishes. Most higher vertebrates have a maximum size. Fish, however, seem to grow continually for as long as they live, if the food supply is

not limited (Weatherly & Gill, 1987). However, linear growth can cease even if height and width continue to increase (Lowerre-Barbierie *et al.*, 1994). Endogenous factors, for example metamorphosis and spawning, as well as extrinsic factors, such as responses to temperature changes, fluctuations in salinity or the availability of food, are likely to influence the structure of the increments (Victor, 1982; Buckley & Blankenship, 1990).

According to Chilton & Beamish (1982) most of the growth in scales occurs prior to the age at maturity. They state that "scales should always be used with the clear understanding that beyond the age at maturity the age of fish may be underestimated". Beamish & McFarlane (1983) emphasised that in older fish, annuli can become very crowded on the edge of the scale, thus preventing a clear identification. The use of scales for ageing has often resulted in the incorrect conclusion that a fish was relatively fast-growing and short-lived. For example, the calculated maximum age of the sablefish *Anoploma fimbria* using scale estimates was 10 years. However, on examination of broken and burnt otoliths the maximum lifespan was shown to be about 50 years (Beamish & McFarlane 1987). Another species, the white sucker *Catostomus commersoni*, exhibit up to 13 years differences between age estimates based on scales and on fin rays (Beamish & McFarlane, 1983). Beamish & McFarlane (1987) provide a detailed description of bias in an estimation using scales in longer lived species.

Most fish are poikilotherms and, therefore, their metabolic rates are directly related to the temperature and hydrographic environments that they encounter (Radtke, 1997). In temperate waters, the seasonal variation in temperature lead to differences in scale growth, with an acceleration in summer and deceleration in winter. The annual groups of striae are, therefore, formed closer together during winter than in summer. However, growth is not uniform between individuals. Temperature and food availability can greatly affect growth. Fish of the same age, for example, will not always be the same length, or vice versa.

Estimation of the age of butterfish requires an unbiased interpretation of the annuli in scales and otoliths. Scales behind the pectoral fin are most useful because they are less likely to be replacement scales. They also tend to be larger and more uniform, which minimises inaccuracies in age assessment. The estimation of fish ages usually involves some error, which can affect management decisions about year-class strength and the effects of fishing on a stock (Hightower, 1996). Therefore, it is important to incorporate ageing errors during stock assessments and to determine the reliability of age data. Both precision and accuracy must be assessed. Precision refers to the reproducibility of results, whereas accuracy describes the degree of closeness to the true value. Validation is an essential step in establishing accuracy, but some indication of precision can be gained by re-reading age structures and comparing the results (Kimura & Lyons 1991; Hightower, 1996).

The aim of this study was to investigate the reproductive biology, social structure and age of *O. pullus*. Aspects of the reproductive biology included a description of the reproductive cycle and colouration, the determination of the onset and duration of the spawning season and evidence for sex change. These results were compared to those of other studies. The relationship between size and age was also examined.

3.2 Materials and methods

3.2.1 Collection of samples

Thirty fish were collected from around the Kaikoura Peninsula during the last week of each month for 13 months. All of the fish sampled were captured by speargun or by gill-nets, using various mesh sizes (2.5", 3.5", 4.5"). Samples were not taken in areas where fish counts were done (see Chapter 2). To catch all size classes, the three mesh sizes were used each month (Hickford & Schiel, 1995). If netting failed to catch

a specific size range, additional fish were collected by speargun. Captured fish were killed on the boat, brought back to the laboratory and stored under cool conditions until the start of the dissection. All fish were processed fresh to maintain the conditions of their internal organs. For each fish, the following measurements were recorded: standard length [SL] (distance from the front of the upper lip of the snout to the last vertebra) to the nearest 0.5 mm, total length [TL] (distance from the front of the upper lip of the snout to the furthest tip of the caudal fin) to the nearest 0.5 mm and weight to the nearest gram. Where visually identifiable from the gonads, the sex was recorded; otherwise, histological examination of the gonads was used to determine the sex.

3.2.2 Histological analysis of gonads

Both lobes of the gonadal tract of all specimens were removed and stored in Bouin's solution for 48 hours for fixation. Gonads were then rinsed under saltwater and transferred into 70% ethanol. For histological staging, a portion of tissue was cut from the middle of one gonad lobe, embedded in paraffin wax, sectioned serially at 10 μm and stained with Ehrlich's Haematoxylin and Eosin. Staging was carried out using an Olympus BH-2 compound microscope. The terminology for the different cell stages was adopted from Forberg (1982) and Hibiya (1982). Terms used to describe the various stages of the oocytes and sperm were modified from Crabb (1993) (Table 3.1 - 3.2).

Photomicrographs were taken using 24 x 36 mm Kodak Ektachrome 64T (EPY 135-36) colour reversal film. All photographs appearing in this section were reproduced from the original photo using a colour-copy machine

Table 3.1 Summary of the stages of oocyte development (modified from Crabb (1993)

Name	Description and occurring changes
Chromatin Stage (CS) Plate 3.1	Many changes to the chromosomes within the nucleus. Nucleoli develop around periphery of nucleus in late stages.
Oil Droplet Stage (OD) Plate 3.2	Appearance and proliferation of oil droplets. Outer zone of the ooplasm shows several vesicles, which are in later stages arranged in a zone between the oocyte periphery and the nucleus. Zona radiata visible in late stages.
Yolk Granule Stage (YG) Plate 3.3	Appearance and proliferation of yolk granules. As vitellogenesis progresses, the yolk inclusions increase in size and number. Zona radiata thickens in later stages. Migration of the germinal vesicle to oocyte periphery. Entire ooplasm fills up with globular yolk masses in later stages.
Maturation Stage (MS) Plate 3.4	Alteration of yolk content, oocytes ready for release (ovulation). Complete development involves a rapid increase in oocyte diameter. Coalescence of yolk globules into a homogeneous mass.
Atretic Oocytes Stage (AO) Plates 3.5 - 3.6	Oocytes become stalled at various stages in their development and undergo subsequent degeneration. Breakdown of cell interior, often spilling into cytoplasm, ovoid shape lost. Post-ovulatory follicles visible.

Table 3.2 Summary of the stages of male spermatogonic development (Plate 3.7)

Stage	Characteristics
Spermatogonia	Large oval cells along the trabeculae; dark-staining, large, nucleus
Spermatocyte	Dark clusters around the trabeculae; nuclear membranes disappear
Spermatids	Spermatocytes after second maturation; smaller more densely packed clusters
Spermatozoa	Spermatids having undergone spermatogenesis; smallest most densely packed stage

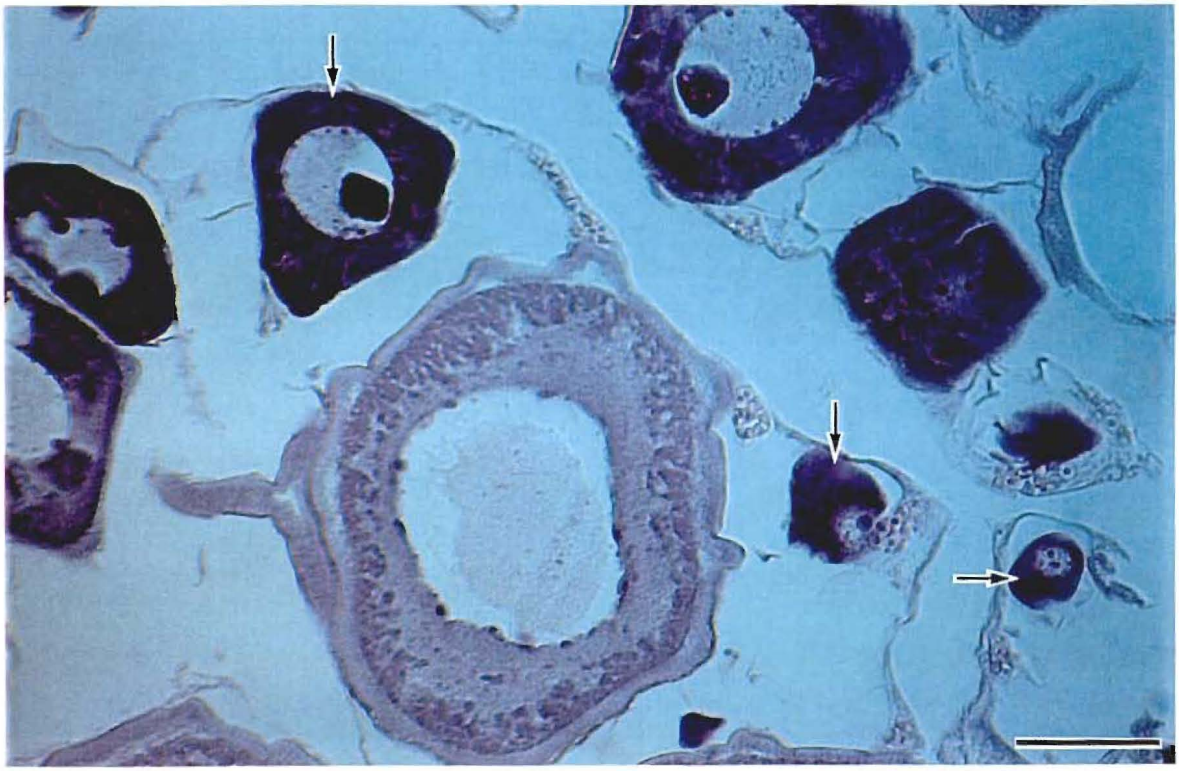


Plate 3.1 Photomicrograph of gametogenic stages taken from histological preparation of *O. pullus* ovary. Example of Chromatin Stage (CS). Arrows indicate early stage oocytes. Scalebar = 50 μm.

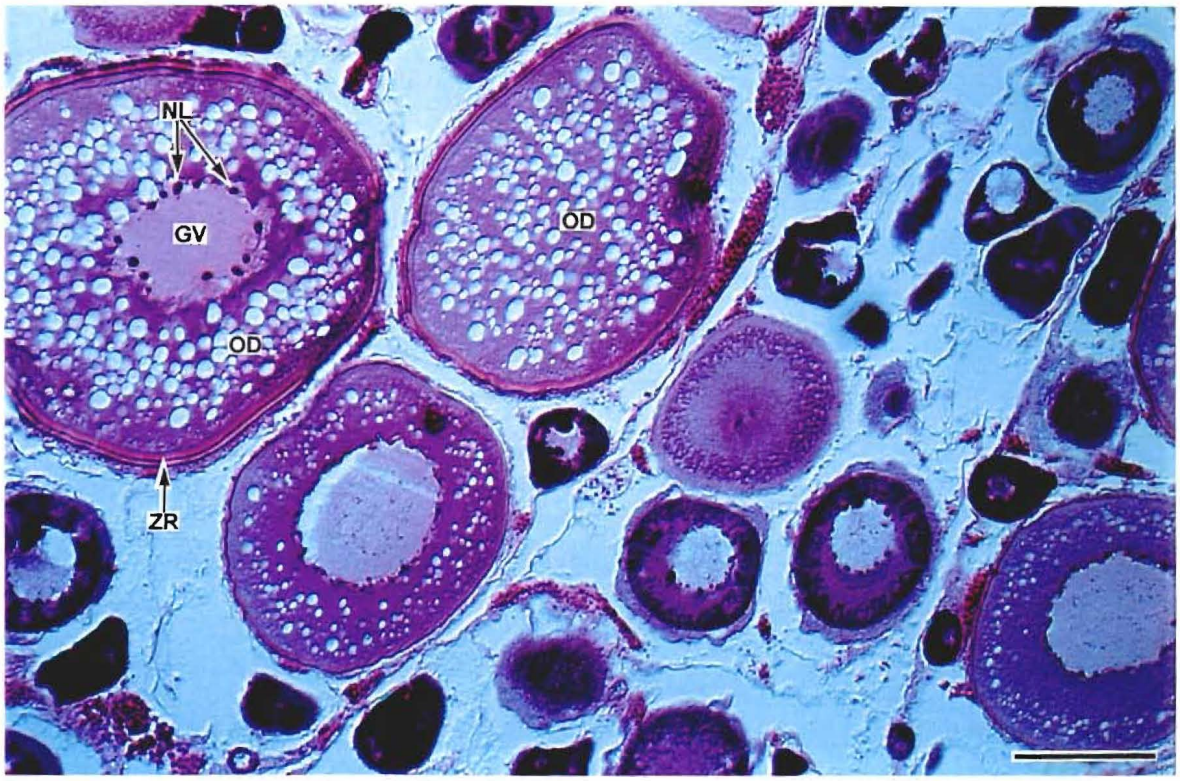


Plate 3.2 Photomicrograph of gametogenic stage taken from histological preparation of *O. pullus* ovary. Example of Oil Droplet Stage (OD). ZR = zona radiata, OD = oil droplets, NL = nucleoli, GV = germinal vesicle. Scalebar = 100 μm.

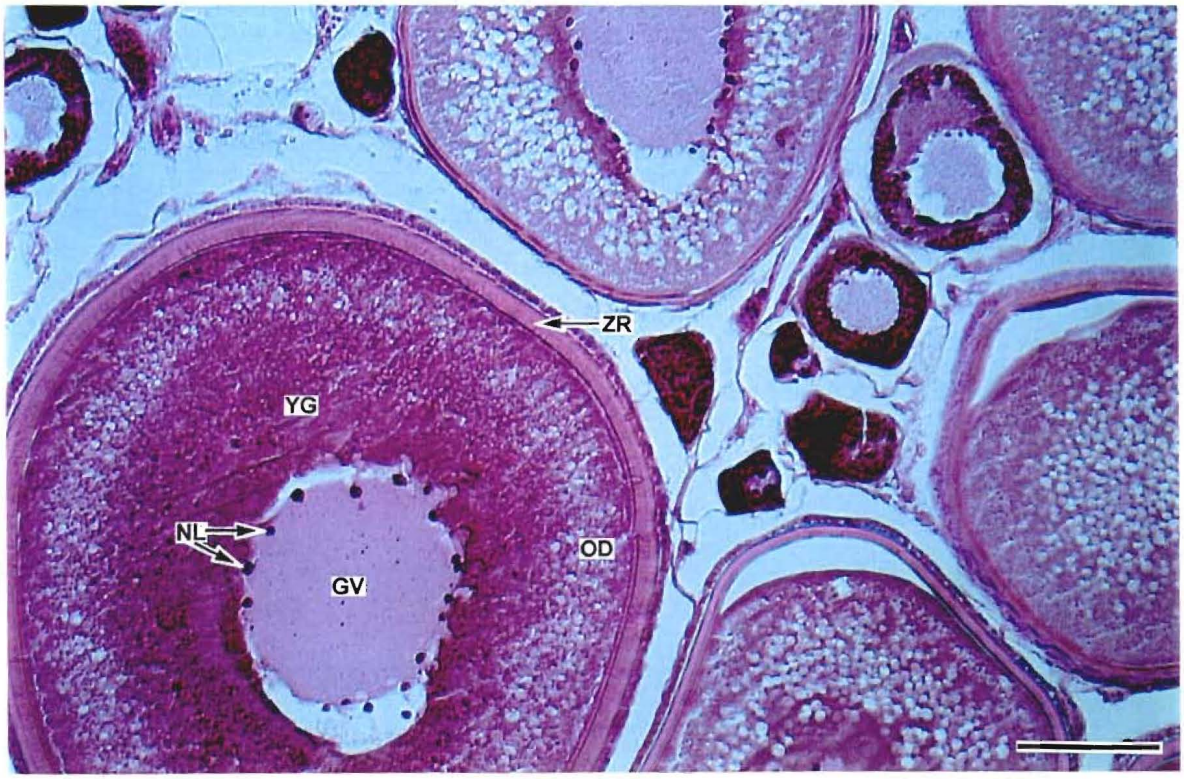


Plate 3.3 Photomicrograph of gametogenic stage taken from histological preparation of *O. pullus* ovary. Example of Yolk Granule Stage (YG). GV = germinal vesicles (with nucleoli at periphery), YG = yolk granule, OD = oil droplets, ZR = zona radiata. Scalebar = 100 μm.

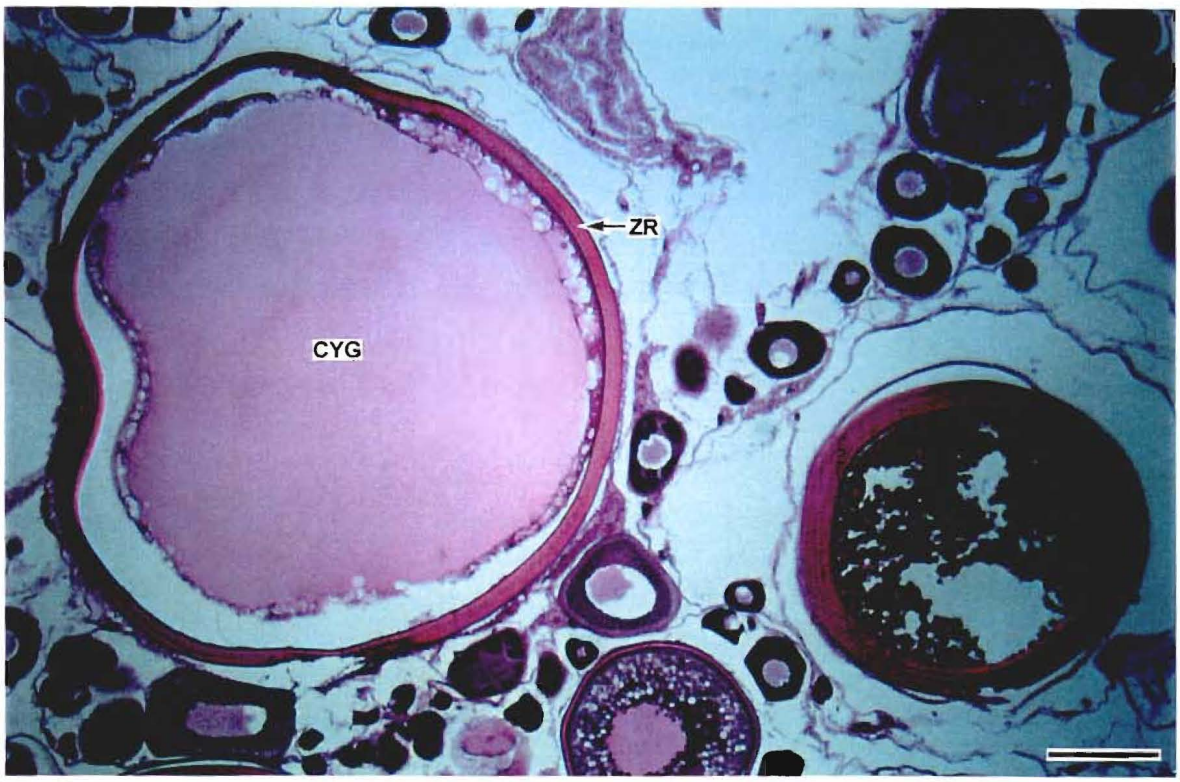


Plate 3.4 Photomicrograph of gametogenic stage taken from histological preparation of *O. pullus* ovary. Example of Maturation Stage (MS). CYG = coalesced yolk granules, ZR = zona radiata. Scalebar = 200 μm.

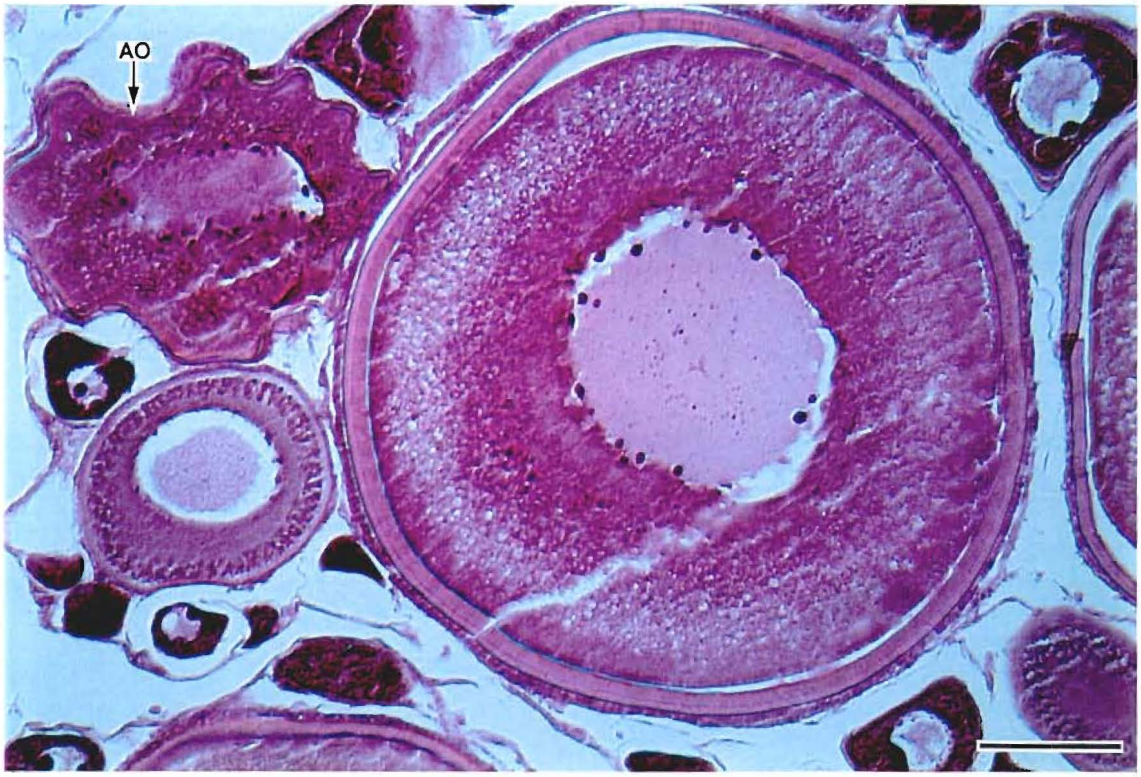


Plate 3.5 Photomicrograph of gametogenic stages taken from histological preparation of *O. pullus* ovary. Example of Atretic Oocyte Stage (AO). Scalebar = 100 μm.

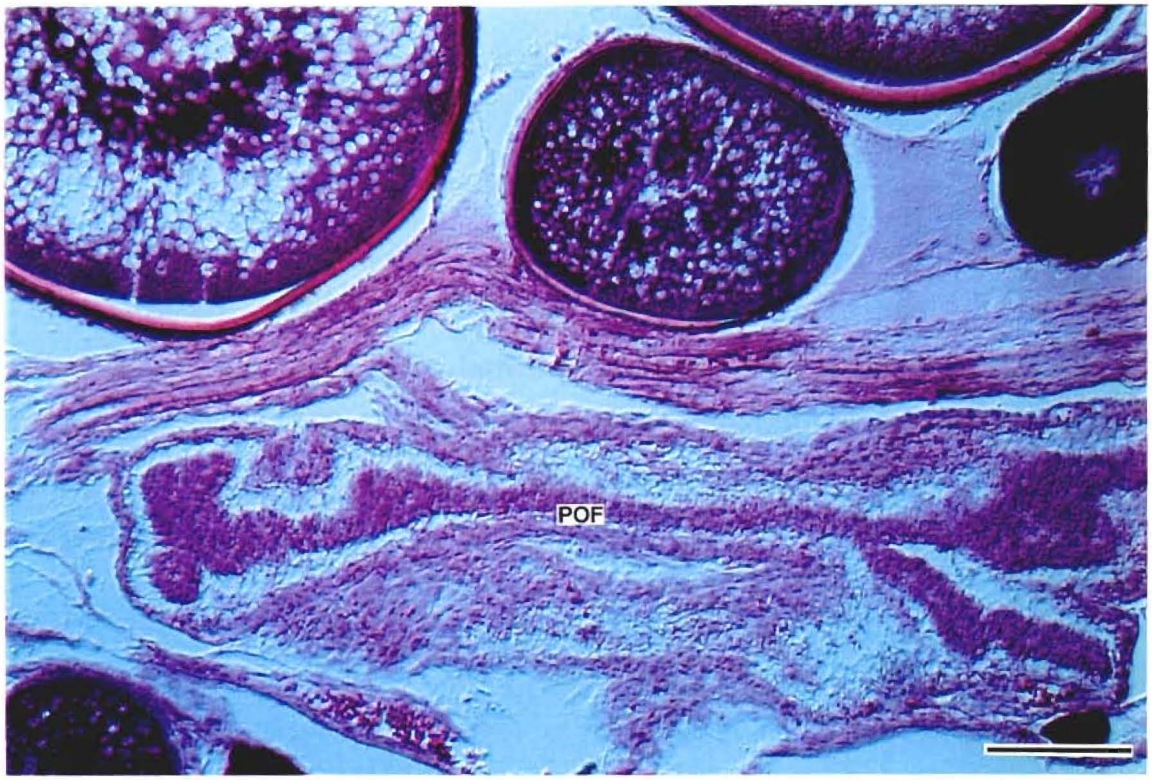


Plate 3.6 Photomicrograph of gametogenic stages taken from histological preparation of *O. pullus* ovary. Example of post-ovulatory follicle (POF). Scalebar = 100 μm.

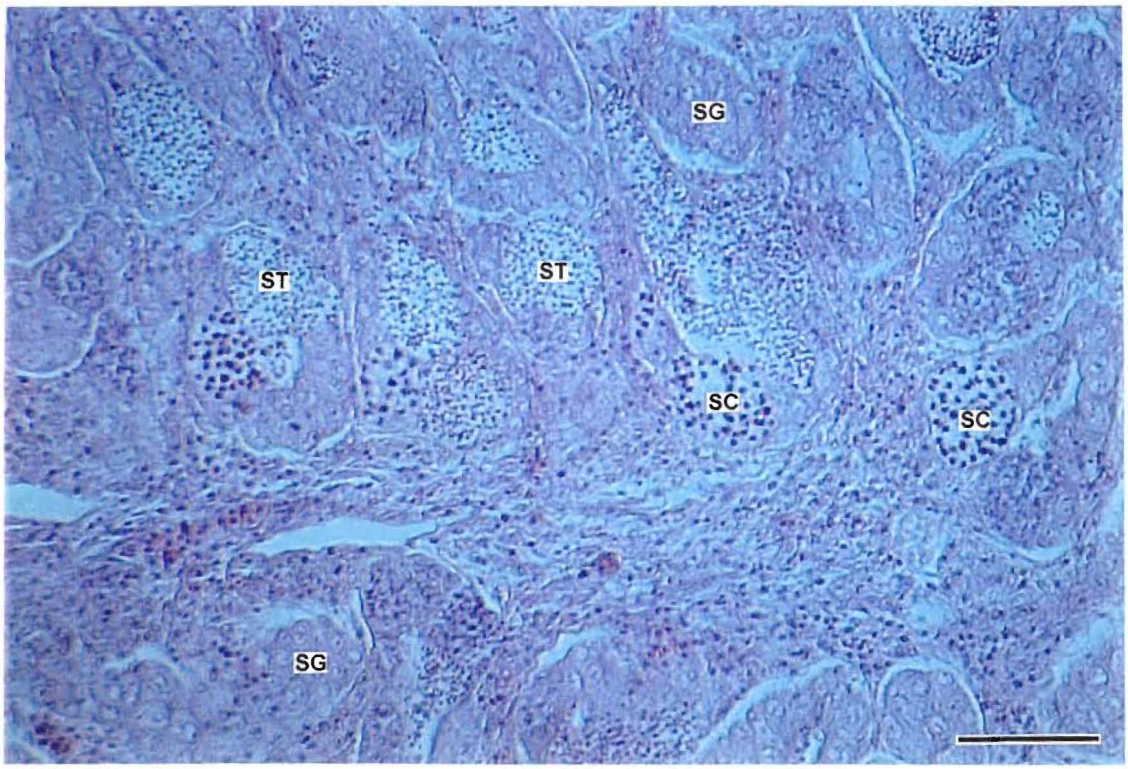


Plate 3.7 Photomicrograph of gametogenic stages taken from histological preparation of *O. pullus* testis. SG = spermatogonia, SC = spermatocytes, ST = spermatids. Scale-bar = 50 μm.

3.2.3 GSI index

There is a linear relationship between body weight and ovary weight in female butterfish (Crabb, 1993). Therefore, the data obtained for individual females were pooled into months and the gonadosomatic index (GSI) was calculated using the following formula:

$$GSI = \frac{gonad\ weight}{body\ weight} x 100$$

A one-way analysis of variance (ANOVA) was done to test the effect of time on the GSI. Data were first tested for variance homogeneity using Cochran's C test and

transformed if necessary. Because of the low number of males caught and the absence of a linear relationship between body weight and testes (Crabb, 1993), no GSI values were calculated for males between September 1996 and January 1997.

3.2.3 Age determination

For age determination, ctenoid scales immediately posterior to the pectoral fin were removed using forceps. Any scales suspected of being replacement scale were discarded. Four to six scales from each side of the fish were removed, air dried and stored. The scales were later read using a slide-projector (Kodak S-AV 1010 projector) and a whiteboard. Scale reading was done as described by Nielsen (1992); it was assumed that each annulus represented one year.

Otoliths were used for cross-validation of the ageing results obtained from scale readings. In 361 specimens, the head was opened with a lateral cut at the dorsal base of the skull, using a sharp knife. To avoid scratching or breaking the otoliths, the whole inner ear was removed. Both organs were extracted and stored in 100% alcohol for later extraction of the otoliths. In this study, only sagittal otoliths were used (Samuel *et al.*, 1987). Further preparation was required to expose the growth increments. Sagitta were extracted from the otolithic membrane (sacculus), using a stereo microscope with 12x magnification and two pairs of tweezers in a shallow petri dish on a black background. Both otoliths were then placed on a clean microscope slide, concave-side up (Watson, 1965; Libby, 1982) and mounted using epoxy raisin.

All otoliths were viewed under a stereo microscope. Two methods were used to count the number of rings. First, the rings of all otoliths were counted under low magnification using the whole otolith. A cold-light source (Schott, KL-1500 electronic) was used to illuminate the otolith (Williams & Bedford, 1974). Fifty randomly selected otoliths were ground down using various grades of wet carborundum paper (1500 grit

to 2000 grit). Grinding continued until the mid-plane of the otoliths was reached and then polished using a felt cloth and toothpaste to remove the grinding marks. All rings were counted in a straight line from the primordium to the otolith's margin. Two counts of all rings in both otoliths and scales were made by a single reader. Fifty randomly selected samples of both scales and otoliths were reread by a second person to test for precision (Pearson *et al.*, 1991).

3.3 Results

3.3.1Sex and colouration

There was a strong bias towards females and juveniles in this study. Of the 450 captured individuals, 293 were females and 111 were juveniles. There were considerable differences between visual sexing and the results of histological examination. Visual sexing showed initially that 36 males were caught but histological examination of the gonad material showed that 19 of these were females with male colouration (see Chapter 1). In total 41 females had very similar colouration to male fish. Four fish were visually identified as males but histological examination showed them to be female. All of the larger fish (> 300 mm SL) had a vivid blue stripe and coloured dots on the side of the head. Females, and some males that were initially thought to be females, had less intense stripes and dots.

There was an apparent relationship between size and colour in juvenile fish. With the exception of thirteen fish, the visual identification of juveniles and small females was confirmed by the histological examination of the gonads. Thirteen individuals were believed to be juveniles but examination of the gonads indicated that they were mature.

3.3.2 GSI index

Cochran's C test showed that the age estimate data were not homogeneous and were therefore transformed using $x'=\sqrt{x}+\sqrt{(x+1)}$ to stabilize variances (Freeman & Tukey, 1950). Although some of the variances could not be stabilised, there were nearly equal sample sizes and the analysis of variance should still be reliable (Glass *et al.*, 1972).

There were significant differences between the GSI over time ($F_{13,407}$ = 30.69, $p < 0.001$) (Fig. 3.1). Between December 1996 and June 1997 all indices showed similar low numbers (Tukey HSD, $p > 0.97$). Thereafter, GSI showed a monthly increase and values in August were significantly higher than in June (Tukey HSD $p < 0.001$), This increase coincided with an increase in water temperature. GSI values decreased again with the onset of summer and values in November were significantly lower than in October (Tukey HSD $p < 0.001$). GSI values for individuals in December 1997 were similar to December 1996 (Tukey HSD, $p > 0.95$). GSI values for males remained low until June and appeared to increase towards June.

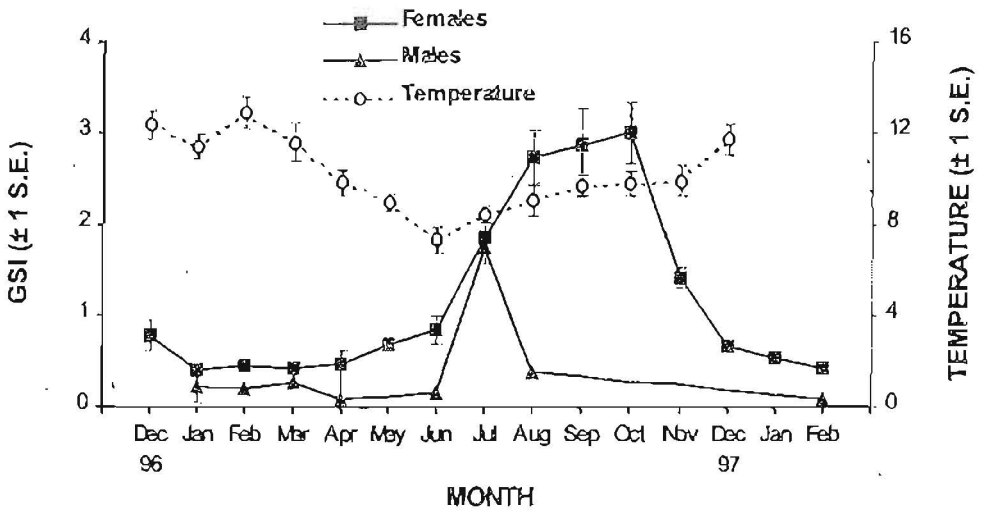


Figure 3.1 Mean sea water temperatures and GSI values for male and female *O. pullus*. Temperature values were obtained during demography study (Chapter 2)

3.3.3 Seasonal ovarian changes

The histological stages and seasonal changes of *O. pullus* gonads from Kaikoura agreed with those described by Crabb (1993). The ovaries of *Odax pullus* consisted of two symmetrical lobes, which were fused anteriorly. Both lobes shared a short posterior oviduct, which terminated at the urogenital opening. The ovarian tissue consisted of multiple ovigerous folds surrounding a central lumen. Gonads collected in December and January showed that spawning had occurred in some fish and was still in progress in others. This was indicated by the presence of hydrated oocytes and post ovulatory follicles (POF). Spawning appeared to have ceased by January as indicated by the absence of vitellogenic oocytes. A definite time for the total cessation of spawning activity could not be established because of the occurrence of POF in some fish during February and March. Although the life span of POF is not known in *O. pullus*, it appeared that resorption followed soon after ovulation. This was also observed by Crabb (1993).

During February and March, the majority of the gonads contained mostly primary oocytes. Atretic and vitellogenic oocytes were rare, indicating that individuals underwent a resting period. Between April and June, ovaries appeared to have undergone a developmental stage, as indicated by the large number of primary and some secondary vitellogenic oocytes. The first occurrence of POFs in some gonads, and the high number of hydrated oocytes in July, showed that the spawning season had commenced and spawning had occurred in some fish.

The size at maturity for female butterfish appears to occur over a range of 200 - 230 mm. The smallest juvenile (150 mm) was captured during peak spawning season (November) and showed numerous primary vitellogenic oocytes but no secondary or mature ones (Plate 3.8). The smallest female showing indications of spawning activity was 202 mm (SL) (Plate 3.9). This fish was caught in June.

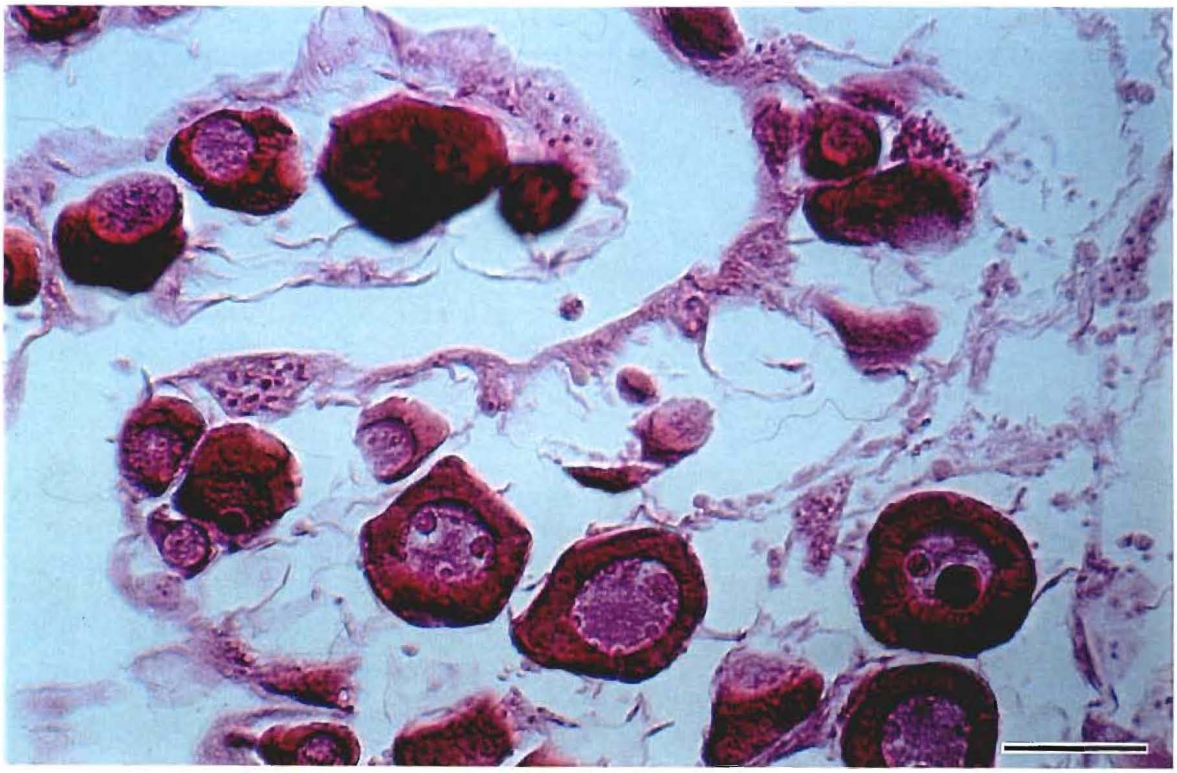


Plate 3.8 Photomicrograph of histological preparation of the ovary of a 150 mm immature juvenile. All oocytes in early Chromatin Stage. Scalebar = 50 μm.

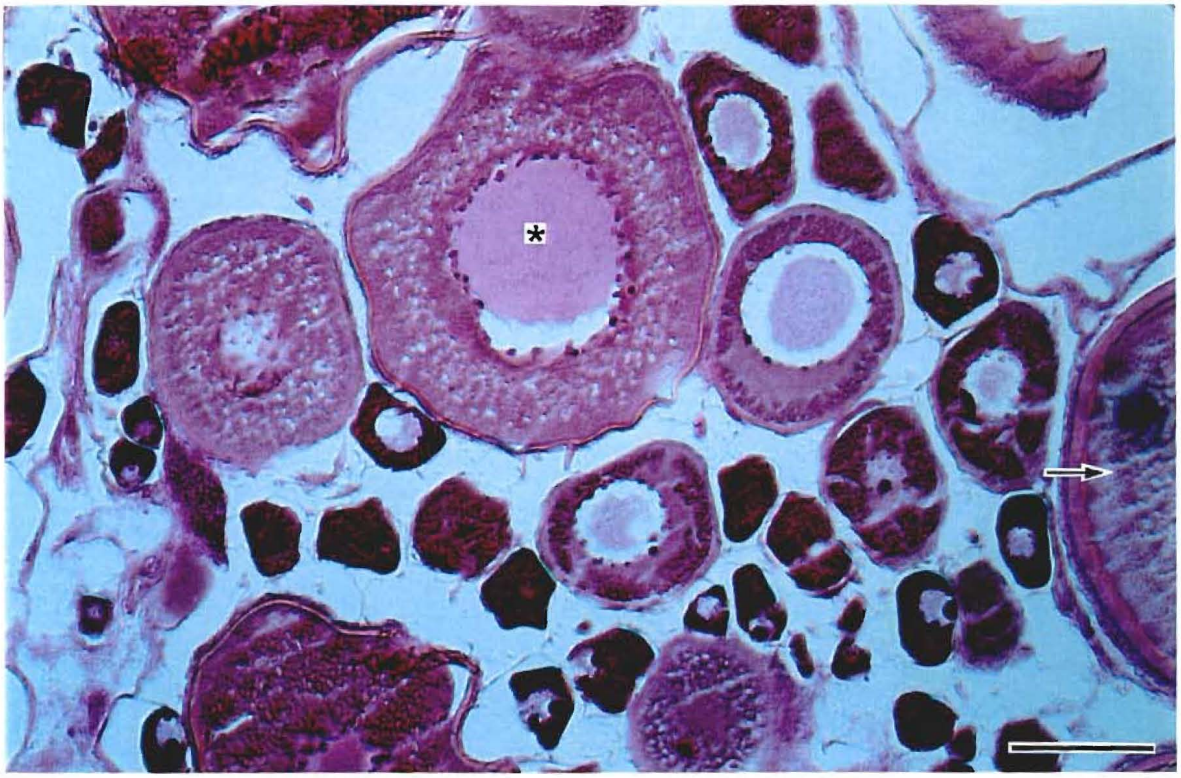


Plate 3.9 Photomicrograph of histological preparation of the ovary of a 202 SL mm female at first maturity. Note presence of Oil Droplet Stage oocyte (*) and partial view of a Yolk Granular stage oocyte (arrow). Scalebar = 100 μm.

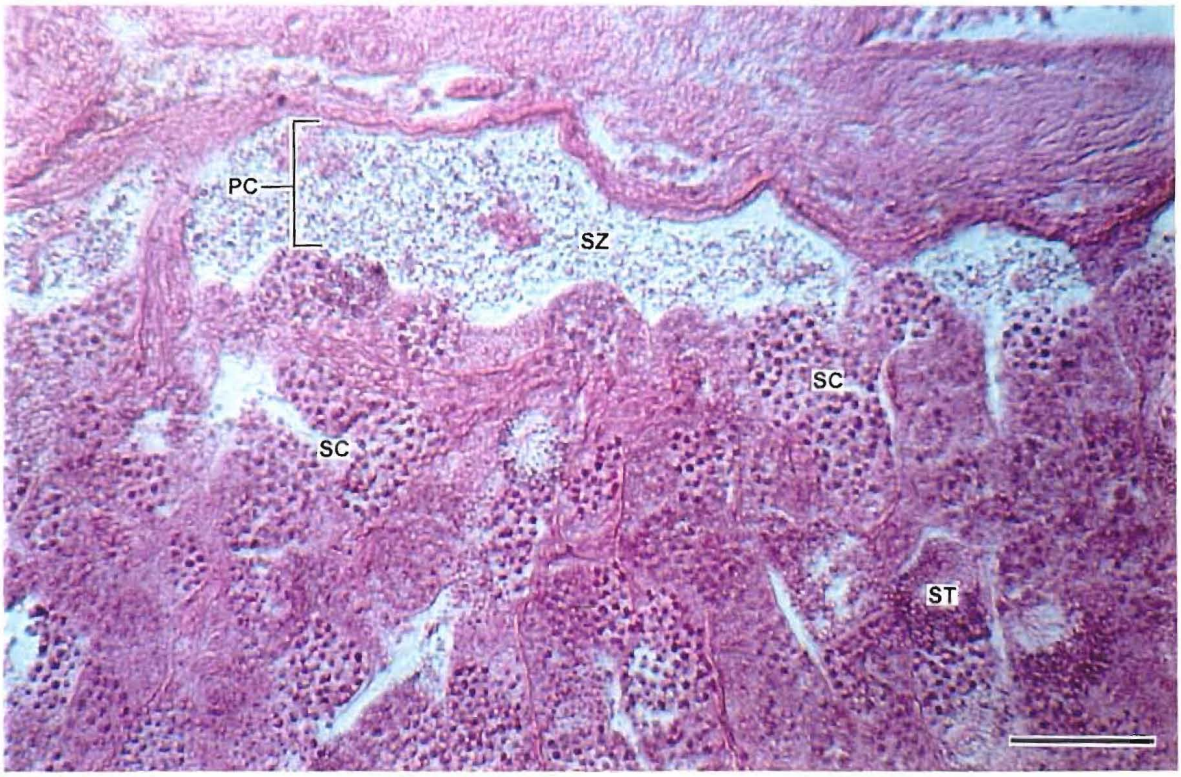


Plate 3.10 Photomicrograph of histological preparation of *O. pullus* testis, indicating sex change. Example showing peripheral crypt (PC). SZ = spermatozoa, ST = spermatids, SC =spermatocytes, SG = spermatogonia. Scalebar = 50 μm.

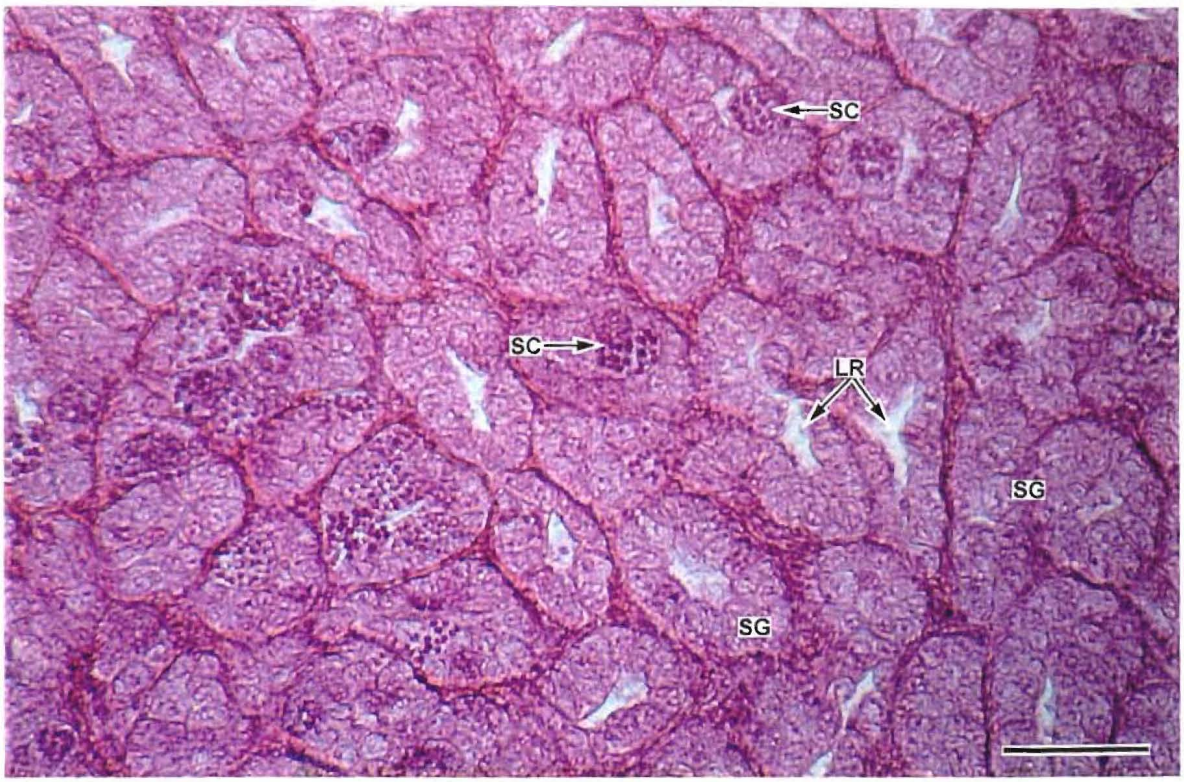


Plate 3.11 Photomicrograph of histological preparation of *O. pullus* testis, indicating sex change. Example showing lumenal remnant (LR). SC =spermatocytes, SG = spermatogonia. Scalebar = 50 μm.

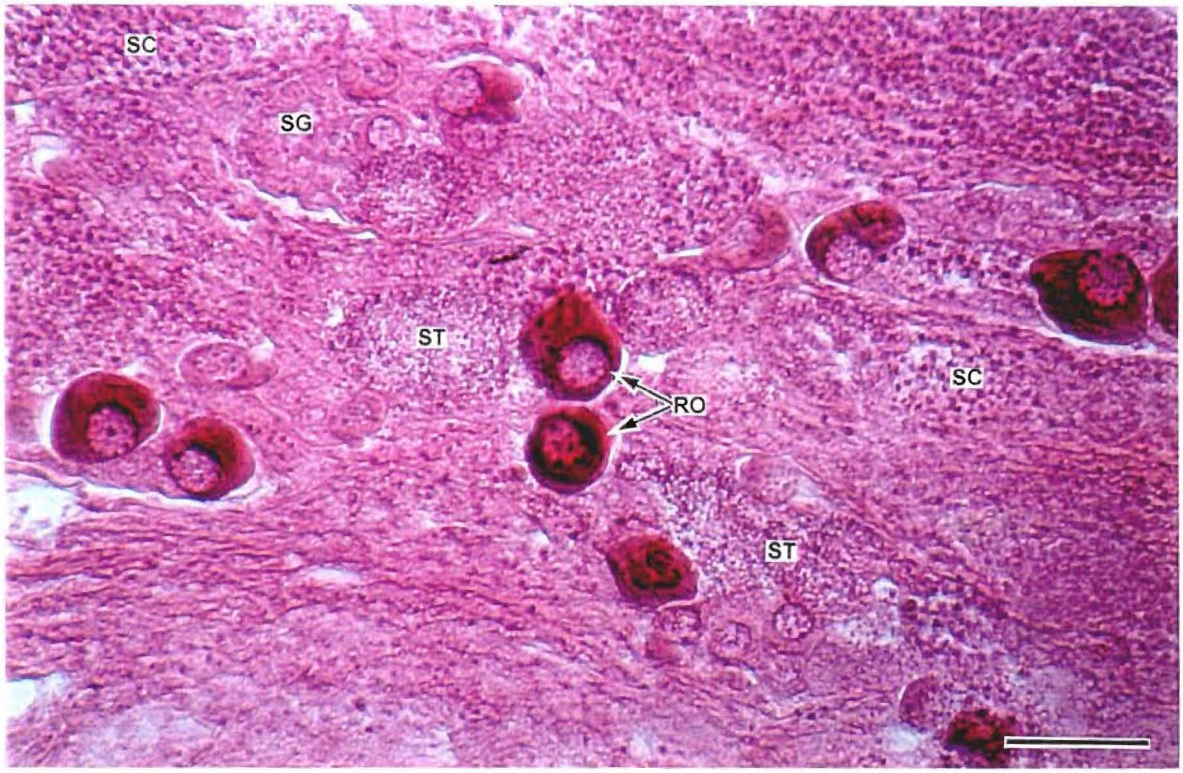


Plate 3.12 Photomicrograph of histological preparation of *O. pullus* testis, indicating sex change. Example showing residual oocytes (RO). ST = spermatids, SC = spermatocytes, SG = spermatogonia. Scalebar = 50 μm.

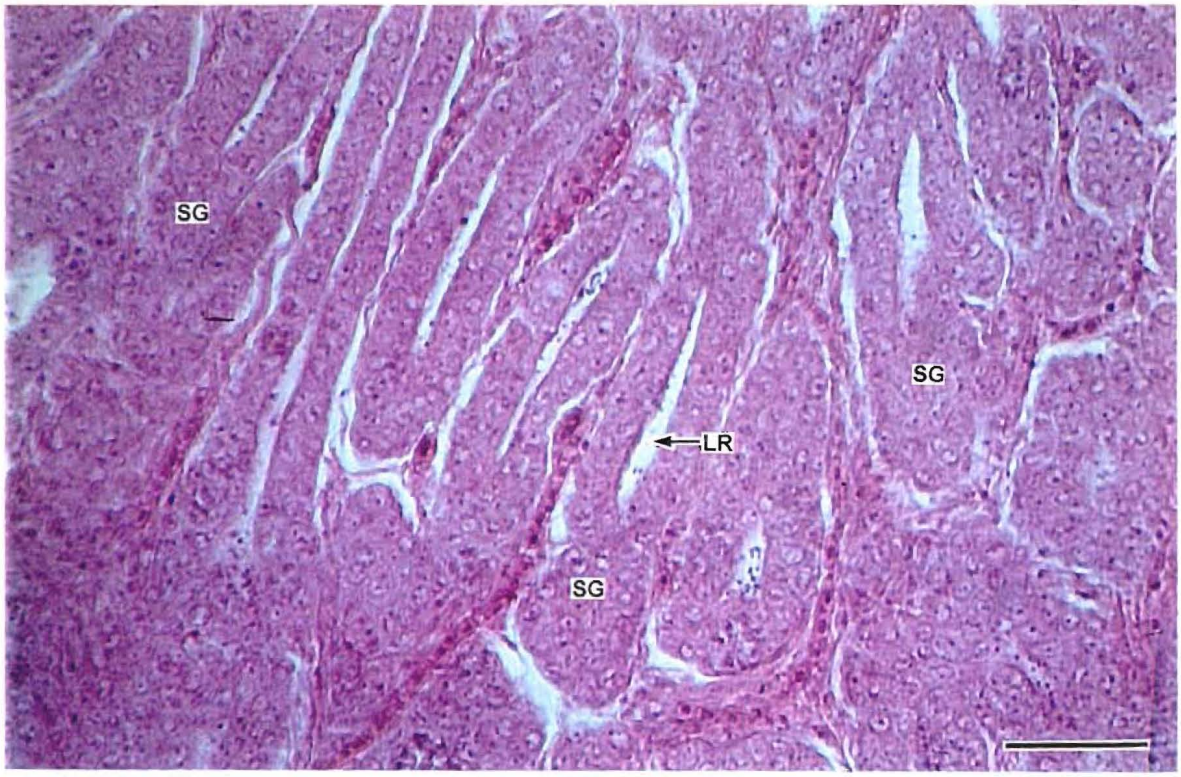


Plate 3.13 Photomicrograph of histological preparation of *O. pullus* testis, indicating sex change. Example showing convoluted lamellar appearance of the testicular material. LR = lumenal remnant. Scalebar = 50 μm.

3.3.5 Age and growth

3.3.5.1 Accuracy of counts

There was a strong correlation between the age estimates of the two readers for both scales (r = 0.91, n = 50) and otoliths (r = 0.90, n = 50) (Figure 3.2). Of the 50 otoliths examined twice, 80% were aged identically and the remaining 20% differed by one year. Scales were aged identically in 84% of all samples examined and the remaining 16% varied by only one year. There was no apparent bias for fish aged 2 - 3 years. An increase in errors occurred with increasing age.

3.3.5.2 Scale vs otoliths

There was generally a good correspondence between age estimation using scales and otoliths (r = 0.62, n = 314) (Figure 3.2).

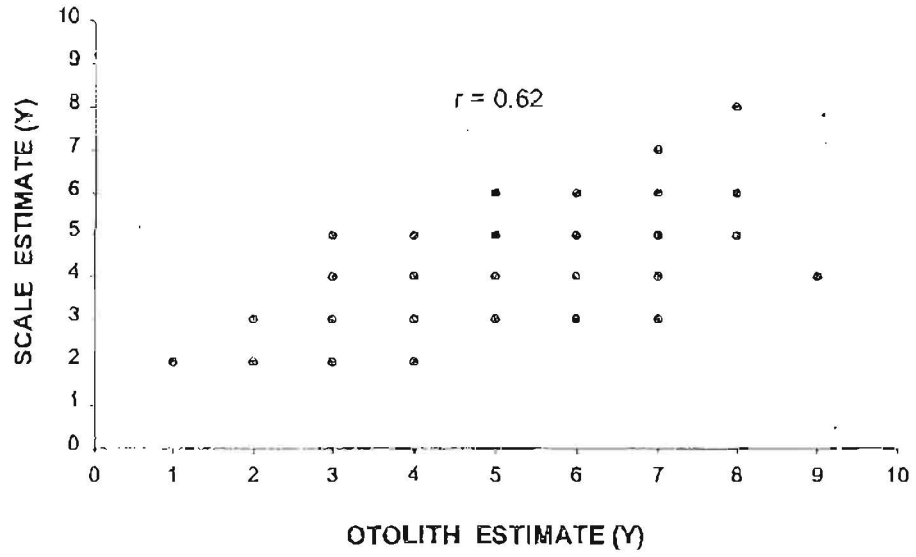


Figure 3.2 Correlation between age estimates of scales and otoliths (n = 314)

Around 45% of the age estimates using scales and otoliths were identical (Fig 3.3). This was dependant on fish size. However, the spread of estimates was greater with increasing fish size. In the smallest size class of fish (< 250 mm), 12% of age estimates using scales and otoliths were within one year of each other. As fish size increased, scales underestimated otoliths by up to three years. Proportional to the increasing age of fish with greater size, however, the degree of accuracy of scales across age classes was similar.

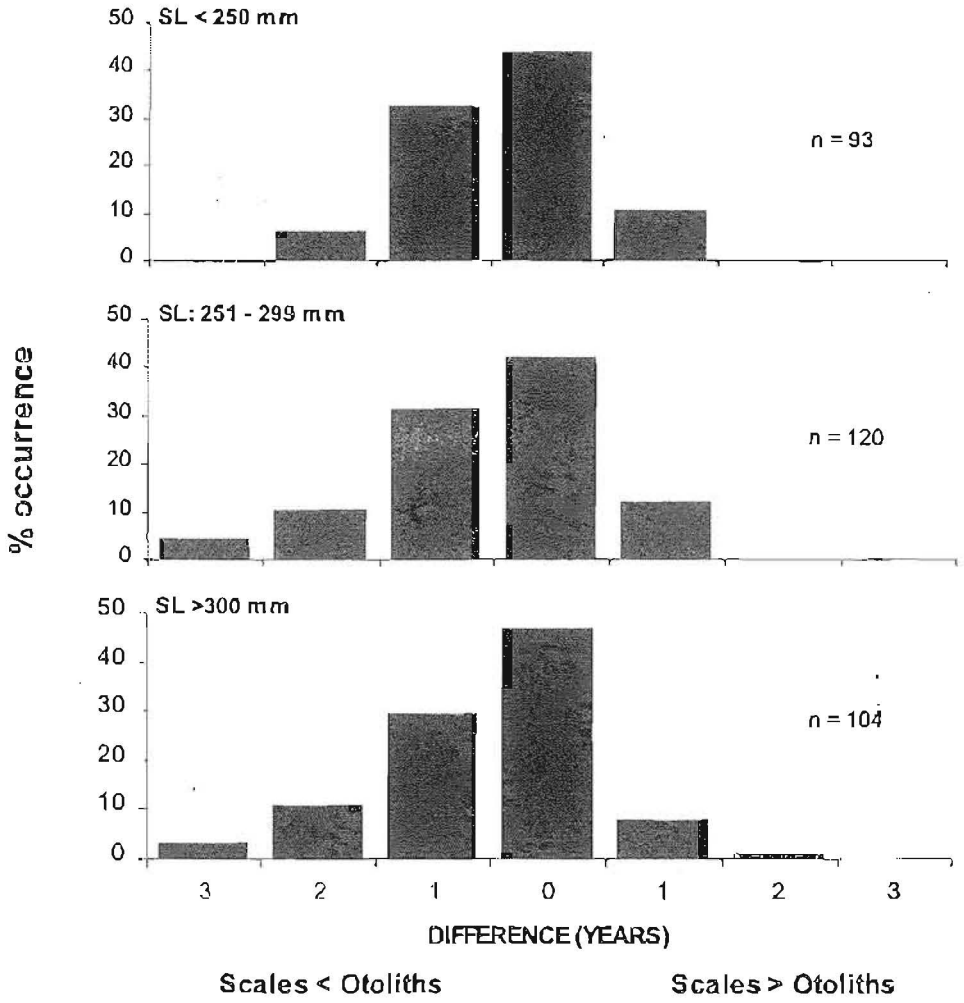


Figure 3.3 Differences in age estimates between scales and otoliths

(n = number of samples)

The comparison of sectioned and whole otoliths showed that there was a close correlation between both estimated ages (r = 0.94) (Figure 3.4). Eighty-two percent of the sectioned otoliths were aged identically to the whole otoliths. Young individuals were more accurately aged than older fish. With increasing age, the accuracy was reduced and in one third of fish older than five, sectioned otoliths showed a higher age estimation by one year.

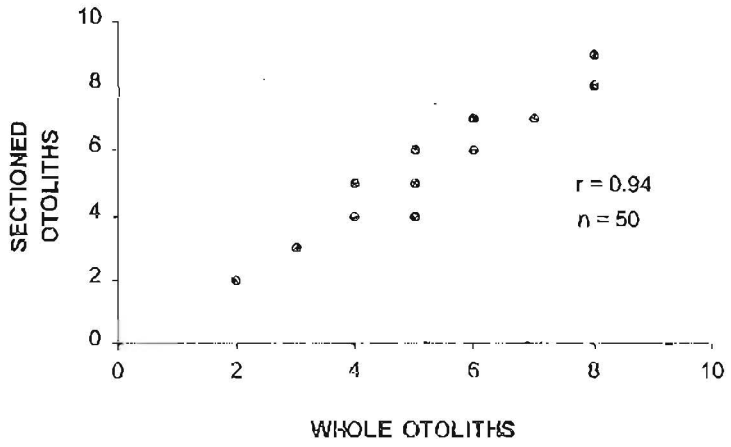


Figure 3.4 Correlation between age estimates determined with whole and sectioned otoliths (n = number of samples).

3.3.5.3 Age and growth

Data from all otoliths and scales (Figure 3.5) were used to calculate von Bertalanffy growth curve parameters (Table 3.4). There were slight differences between the two calculated von Bertalanffy curves. The estimated size calculated from scales was higher than for estimates derived from otoliths data. This size discrepancy increased gradually with age. For example, at age four years, otoliths indicated a size of 276 mm while scales indicated a size of 286 mm.

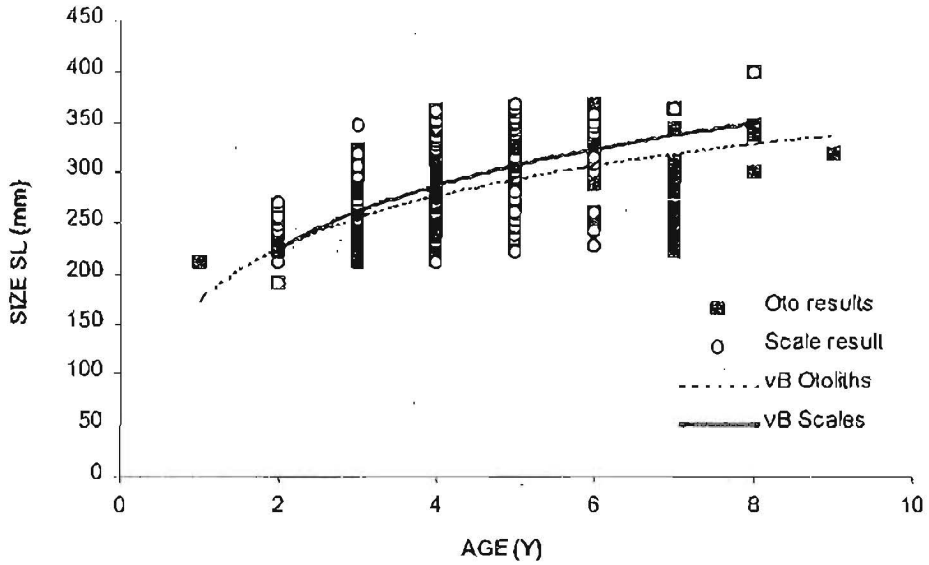


Figure 3.5 Raw age-length data and the calculated von Bertalanffy growth curve for all sampled fish using otoliths and scales. (vB = fitted von Bertalanffy growth curve)

Table 3.4 Calculated von Bertalanffy growth curve parameters for *O. pullus*

	Scales	Otoliths
L_{inf}	375.991	365.511
t_0	-1.399	-2.395
K	0.2667	0.2201

There were large variations in size among fish of apparently the same age (Figure 3.6). This variation was most likely due to the fact that part-year growth was not incorporated into the analysis. Thus a fish designated as age two could have been between 730 and 1094 days old.

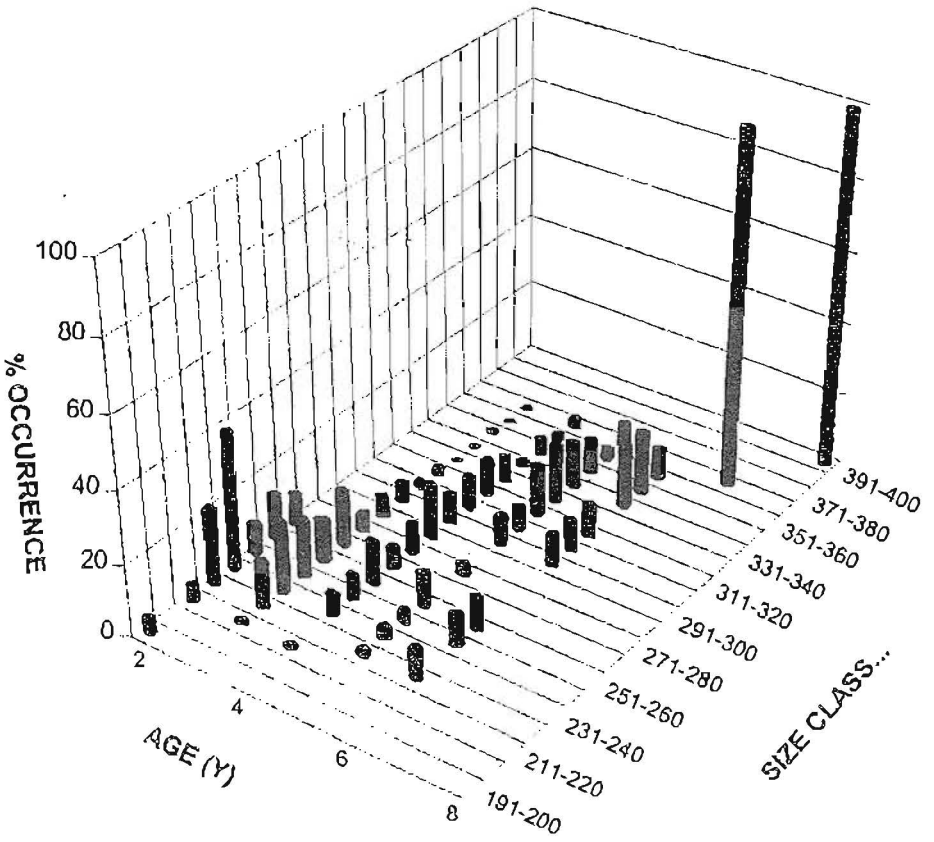


Figure 3.6 Percentage size-age distribution of *O. pullus*

There was a clear trend in ontogenetic stage with both size and age (Figure 3.7). All fish ≤ 200 mm (SL) were juveniles, although some juvenile fish were as large as 300 mm (Figure 3.7 a). Most juveniles were two or three years old but a small proportion was age four (Figure 3.7 b). Mature females ranged from 200 - 350 mm (SL), but varied considerably in age, ranging from 2 - 6 years old. There was a clear separation in sizes between female and male fish. The largest fish, those > 300 mm (SL) were all males. In the fish sampled, there was some overlap in ages between males and females, with males ranging from 4 - 6 years old. The oldest fish found (not shown in graph) was a nine years old and 385 mm (SL).

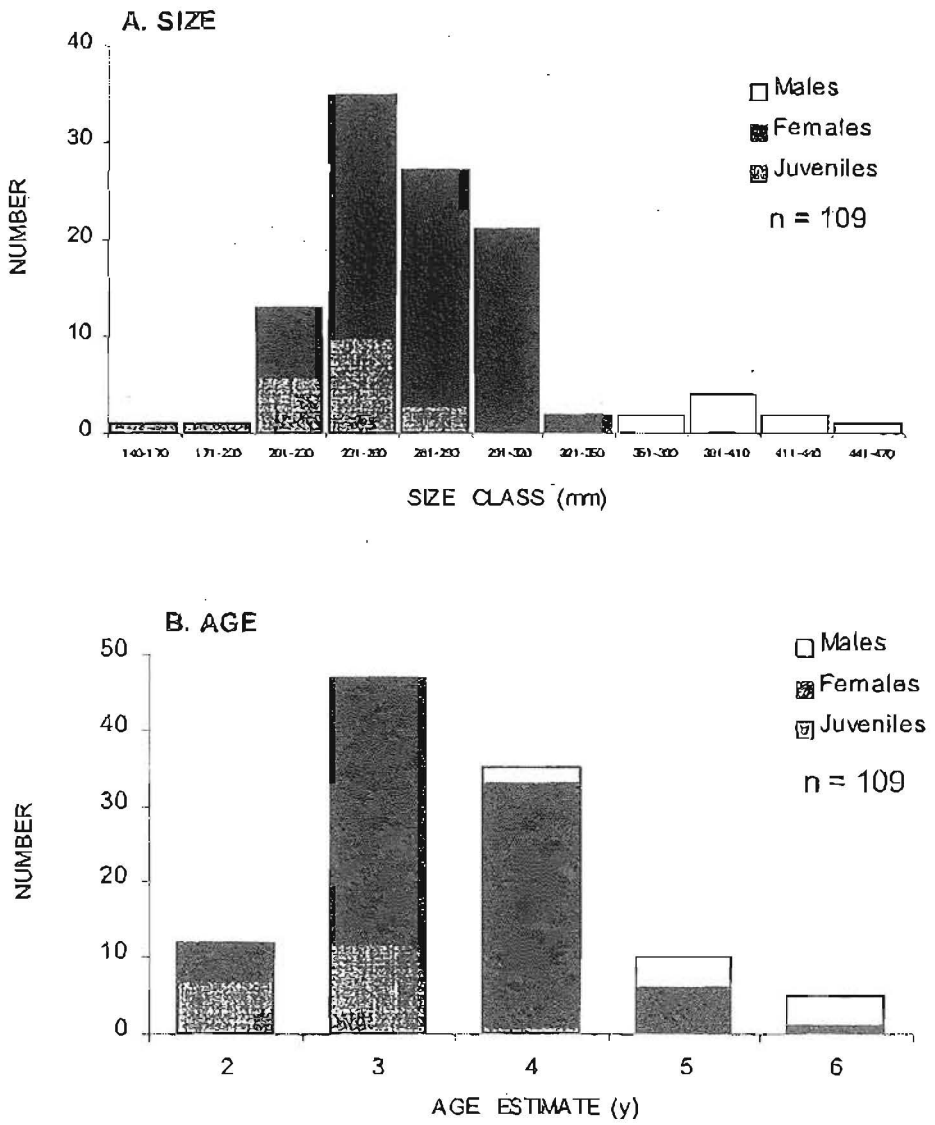


Figure 3.7 Age and size frequency of *O. pullus* caught between December 1996 and March 1997 (n = total number of fish caught).

3.4 Discussion

3.4.1 Reproductive seasonality

The development of oocytes within the gonads was synchronous for all mature female butterfish. The GSI remained at an elevated level for an extended period. This indicates the occurrence of multiple spawning events, rather than the release of a single large clutch of oocytes on one occasion. In the case of a single spawning event, the GSI would have shown a sharp drop and the majority of gonads would have appeared spent. The considerable decrease of the GSI between October and December indicated that spawning ceased at the end of the year. According to Crabb (1993), this drop-off in GSI is the consequence of decreased recruitment of primary phase oocytes into vitellogenesis.

De Vlaming *et al.* (1982) stressed the importance of adequate verification before the GSI can be used as an index for gonadal activity. During this study, highest GSI values were recorded when all oocyte stages for females were present, which verifies that GSI values are a good indicator of spawning (Crabb, 1993). However, histological data provide a better estimate of the reproductive events. The stages identified from the histological examination in this study corresponded to those described for *O. pullus* by Crabb (1993) and those of other species (e.g., Mayer *et al.*, 1990). Three distinct periods were recognisable: development (April - June), spawning (July - December) and a quiescent period (January - March).

During the developmental phase large numbers of oocytes in their primary growth phase were present. Towards the end of the developmental period, increasingly more fish showed small numbers of primary vitellogenic oocytes. June marked the end of the maturation phase, with large numbers of primary vitellogenic oocytes and the first appearance of secondary vitellogenic oocytes. Most fish captured between July and November had hydrated oocytes and post ovulatory follicles (POF), indicating that

spawning had occurred. The increased occurrence of atretic oocytes and POF by late November indicated that in the majority of fish spawning had ceased. This was supported by the rapid decline of the GSI for that period. Thereafter, all remaining vitellogenenic oocytes were invaded by granulosa cells which phagocytose the remains (Dipper & Pullin, 1979).

Fish collected between December and January showed evidence of a quiescent period, which supports the assumption made by Crabb (1993). Resting periods in gametogenesis have been shown for other teleosts (Crossland, 1977; Young *et al.*, 1987). However, in contrast to other species, butterfish appear to have a period of decelerated gametogenesis, rather than a complete cessation. Throughout the resting period some individuals showed oocytes at the chromatin- and oil droplet stage, indicating that oocytes may be produced throughout the year, with some periods of slow oocyte development.

Decelerated oocyte growth may be related to nutrition (Hubbs *et al.*, 1968). Similar to most percoid fishes (Nikolsky, 1963), *Odax pullus* accumulate storage fat, mainly around the alimentary tract, prior to the onset of spawning (Ritchie, 1969). The start of the spawning season in July coincides with the highest amount of deposited fat (Ritchie, 1969), which are believed to provide energy reserves for the increased requirements during oocyte development (Doak, 1972). Therefore, retarded oocyte growth may be partly caused by the allocation of most energy to the rebuilding of fat reserves.

The timing and duration of the reproductive season may have been influenced by photoperiod, diet (see Chapter 4) and water temperature. Ritchie (1969) showed that Wellington populations spawned until late February. Crabb (1993) found the spawning period to be shorter for fish in the colder waters of Otago. During this study GSI values increased with increasing water temperatures. An increase in sea temperatures increases primary production (Tardent, 1979), which should enhance survival and

growth of offspring. Wooster & Bailey showed one of the major determinants of survival during early life history is starvation. Early spawning events could also be advantageous because of the increased availability of food for newly recruited juveniles.

3.4.2 Size and colouration

Odax pullus populations around Kaikoura exhibit three distinct colour phases but there seemed to be no marked sexual dichromatism in larger fish. Therefore, larger individuals appear to be monochromatic rather than dichromatic. This suggests that in female butterfish, colour phases similar to labrids may be applicable. Smaller females (reddish-brown) could be identified as the initial phase (IP), whereas larger ones (darker green/brown) could be categorised as terminal phase females (TP). This indicates that general colour patterns in older fish may not be as important as other patterns, such as chin markings.

Ritchie (1969) observed that during the spawning season, males showed increased intensity of chin markings and female markings remained similar throughout the year. The intense colouration of a terminal male fish is important for positive gender recognition (Crabb, 1993), especially in pair spawning where rapid recognition of species and sex is important (Choat & Robertson, 1975). Intense colour patterns are often an indication of increased fitness, making the individual more attractive. Because males establish loose territories during the spawning season, attractiveness may only be of secondary importance and intense colouration may be used in aggressive behaviour towards other males. The fading of the head markings in all fish outside the reproductive season could be related to predator avoidance. Seals, for example, are visual predators, and brighter colouration of fish may increase the risk of predation.

The incorrect visual identification of females as males may have been caused by the delay in the development of male characteristics. Alterations in body elements, such as fin length, may take longer than morphological changes of the gonads or behavioural adaptations. Choat & Robertson (1974) showed changes in the behaviour of the largest females immediately following the removal of the dominant male, whereas colour and gonadal changes took place at a later stage. Therefore, some males may have been captured after the gonads had changed but before any external morphological changes were obvious. Delayed changes towards external male characteristics may ensure the maximum allocation of energy towards gonadal transformation.

3.4.3 Sex change

This study confirms that *Odax pullus* exhibit protogynous sex change. There are several factors suggesting protogyny in fish. These are the absence of primary and small males, bimodal size frequency with males generally larger that females, primary oocytes within the testes and vestigial lumen in testes.

Distinct colour changes after sex reversal have been demonstrated within the Labridae (e.g. Reinboth, 1970; Jones, 1980). Robertson & Choat (1974) showed that in the dichromatic diandric moon wrasse *Thalassoma lunare*, the colouration between males and secondary males and between females and secondary males differed considerably. Thus, if small primary males did occur in butterfish populations, any colour differences are likely to be similarly as distinct (Crabb, 1993). However, the colour patterns of *O. pullus* observed in this study were more similar to monandric species, such as the cleaner wrasse *Labroides dimidiates*, which has monochromatic adults but shows distinct differences in colour between adults and juveniles (Robertson, 1974).

Sex reversal in fish usually occurs during a transitional period, in which the animal is unable to reproduce as either sex (Crabb, 1993). Therefore, sex change usually takes place during non-reproductive periods to ensure the maximisation of reproductive fitness. Robertson (1972) showed that in labrids the time span for sex reversal was adaptive. Butterfish may also change sex when a reproductive advantage is achieved. All of the individuals exhibiting signs of recent sex reversal were caught during the non-reproductive period (July to October) prior to any development of active reproductive tissue.

Nine out of the 17 males caught had residual oocytes within the testes. These were randomly scattered throughout the gonad and there was no evidence of vitellogenesis. Histological results indicated that the testes of *O. pullus* show similarities to secondary testes of other species, such as *Sacura margaritacea* (Reinboth, 1963). All males showed a secondary *vas deferens* in the testes wall. The secondary derivation of the *vas deferens* appears to be present in all protogynous fish (Hourigan & Kelly, 1985) Reinboth (1962) showed that these newly formed sperm ducts are typical of secondary testes and are only found in males derived from females. Similar results were found in scarids (Choat & Robertson, 1975).

During this study, no small males (< 30 cm) were either observed (Chapter 6), counted (Chapter 2) or caught (Chapter 3), which suggests the absence of primary males in the butterfish population. Most protogynous species have a sex ratio biased towards females, which is usually caused by the differences in mating success of territorial males (Warner & Hoffman, 1980). Gillanders (1995 a) showed that the female-biased sex ratios in the blue groper *Achoerodus viridis* reached up to 62 : 1 at some sites. In my study, the sex ratio of all fish caught was 39 : 1 (females and juveniles: males). Biased sex ratios may act as an inbreeding mechanism that decreases the number of genotypes available for recombination, thus allowing the best adaptation to local conditions (Choat, 1969). However, unequal sex distribution cannot be seen as definitive evidence for hermaphroditism (Sadovy & Shapiro, 1987). Factors such as

varying growth rates and mortality between sexes may also influence population structure and sex distribution.

The significance of sex change is still unknown but it is likely to be influenced by social stimuli. Shapiro & Lubbock (1980) suggested that some females may change sex when a threshold size is reached or when females greatly outnumber males. The hypothesis that sex reversal is induced upon reaching a certain size does does not consider the various other factors that have been linked to sex change. Strong evidence exists that a variety of social factors can initiate sex change and this is valid for loose social groups (Ross, 1990) and harem assemblages (Robertson, 1972; Aldehoven, 1986). Within many reef fish species the removal of the dominant male triggers a sex reversal in the largest female (e.g. Fricke & Fricke, 1977; Warner, 1982; Nemtzov, 1985; Warner & Swearer, 1991).

3.4.4 Ageing

Scales and otoliths have been used extensively for age determination, while recent studies have shown that estimates using scale readings frequently underestimate the age, especially in older fish (Carlander, 1987). Chilton & Beamish (1982) stated that each stock or population has to be validated separately and that all ages need to be validated. Calcified structures should be examined in small juveniles and adults to determine the location of the first annulus.

My study has shown that osseochronometry using scales and otoliths is a satisfactory method for aging butterfish, at least up to the age of six years. Even though there were discrepancies between ages from scales and otoliths, within all size classes 84% of the estimates were within one year of each other. Often, scales were shown to underestimate the actual age of the individuals. This is similar to the results of Erickson (1979) and Sikstrom (1983) who found that in Arctic grayling *Thymallus*

arcticus ages determined from otoliths was consistently greater than those obtained from scales. Barnes & McFarlane (1984) (cited in O'Gorman *et al.*, 1987) showed that ages of lake whitefish *Coregonus clupeaformis* based on otoliths, showed similar tendencies but occasionally indicated younger ages.

Whole-view otoliths examination can provide an accurate method for aging *O. pullus*, at least to age six. However, because of the decreased accuracy in older fish, whole-view examination does not appear suitable for the determination of maximum age. Hoyer *et al.* (1985) showed that in largemouth bass, *Micropterous salmoides*, young fish were accurately aged when otoliths were examined in whole view. However, age determination in older individuals required sectioned otoliths to ensure correct results. Maceina & Betsill (1987) showed similar accuracies in the white crappie *Pomoxis annularis* when using whole otoliths.

Because very few butterfish older than seven were caught, there was no indication whether scales and otoliths are accurate enough for a precise age determination in older individuals. Paul (1976) showed that in smaller snapper, *Chrysophrys auratus*, scales and otoliths provided similar results. However, above the age of 12 there was virtually no agreement because otoliths frequently showed more rings than scales did. Large male butterfish are believed to show decelerated growth, therefore, scale data should be treated with caution, as scales of larger fish frequently underestimate the actual age in older individuals (Beamish & McFarlane, 1987).

In comparison to some temperate reef fish species such as red moki, *Cheilodactylus spectabilis*, which reach ages of 80+ years (Choat pers. com.), *O. pullus* is a rather short-lived species. Because of the small number of large males caught, the maximum age of *O. pullus* could not be conclusively established. The largest fish examined (393 mm SL) had an estimated age of 8+ years. However, the oldest fish (9+) measured only 385 mm (SL). This corresponds to the results of Crabb (1993) who showed the same ages for fish with similar sizes but other studies, such as Ritchie (1969) and

Paul (1997) showed 8 - 9 years old fish to range between 470 and 570 mm SL. The relatively poor fit of some length-age data to the calculated von Bertalanffy curves can probably be explained by inter-annual variation in growth rate.

The range of fish lengths at a particular age is wide. Some fish have almost certainly been aged incorrectly. However, because all data were pooled, seasonal growth was not taken into account. Seasonal differences in growth are caused by various biotic and abiotic factors. Fluctuations in water temperature have been shown to influence growth rates in the Arctic cod *Gadus morhua* (Jørgensen, 1992) and may have also affected inter-annual growth rates in butterfish. An extended spawning season in some in individuals may have also contributed to size differences within year classes (Horn, 1996).

Because no fish younger than two years were caught, there was no information on growth between first settlement and the age of two. However, the growth curve suggests that *O. pullus* grow rapidly over the first two years, reaching approximately 200 mm in length. Thereafter, growth appears to decelerate slightly and individuals appear to grow at a steady rate with no pronounced levelling off in older fish. The initial deceleration may be caused by an increased energy allocation towards reproduction.

Butterfish in Kaikoura appear to mature at an earlier age than suggested in previous studies. Maturity occurred around 200 mm, or between the age of two and three, which are considerably lower than the results of Ritchie (1969) and Crabb (1993) who estimated maturity to occur at age five. However, those studies were characterised by few small individuals. Some labroid species appear to require a certain minimum size rather than age before maturity occurs. Jones (1980 b) showed that spotties from different geographical areas matured at the same size, but showed considerable differences in age. Individuals from northern New Zealand matured after their first year at around 110 mm, whereas fish from the colder waters of Wellington remained

immature for 2 - 3 years before reaching a similar size. The study of small butterfish from different locations may, therefore, provide a better insight variation in the age at first maturity.

The growth rates and maximum size estimates at certain ages are considerably lower than previously suggested by Ritchie (1969). This may be due to latitudinal variations between populations. Jones (1980 b) found that spotties, *Notolabrus celidotus*, from different geographic populations showed significantly different growth rates. Because of the low number of *O. pullus* males caught, it was not established whether growth rates vary between large females and males.

This study has shown that *O. pullus* have complex life history traits related to factors such as season, social systems and age. However, there are still aspects of butterfish life history that require further investigation, for example the relationship between diet and reproduction and the verification of the abundance of superfemales. Field observations of social groups, following the removal of the dominant male and histological examination of individuals with suspected sex reversal, would improve the knowledge of the social influence on the mechanisms of sex change. Further studies on age determination, especially in older fish, may help clarify differences between geographically separated populations.

CHAPTER FOUR

Feeding

4.1 Introduction

4.1.1 Herbivory in fish

Herbivory in marine fish has been of considerable interest in recent years (Clements & Bellwood, 1988). Most of this interest has focussed on the general evolutionary and ecological questions surrounding fish herbivory. Gerking (1994) suggested that wherever adaptive radiation has occurred, piscine herbivory has developed. As a result, herbivory has evolved independently in at least 44 families, utilising a broad range of algae.

The wide variety of different food sources used by herbivorous fish is well reflected in the Cichlidae. Within this family there are phytoplankton feeders *(Tilapia esculata),* periphyton feeders *(Hemitilapia oxyrhynchus),* macrophyte feeders *(Oreochromis rendalli* and O. *zilh),* and various benthic algae feeders, such as rock scrapers *(Pseudotropheus tropheus),* rock combers (P. zebra), nippers on filamentous algae *(P. fuscus),* and sand scoopers *(Gephyrochromis moonS.* The majority of studies investigating piscine herbivory have focussed on tropical environments, but recently several studies have concentrated on herbivorous fish in temperate waters (e.g. Russell, 1983; Horn *at al.,* 1986; Meekan, 1986; Clements & Bellwood, 1988; Clements, 1991 a,b; Horn & Neighbors, 1991; Clements, 1992; Horn, 1992; Clements & Choat, 1993).

Russell (1983) examined the feeding habitats and dietary requirements of fifty species of fish around the coast of New Zealand and concluded that carnivorous species were the most abundant group (88%), followed by herbivores (10%) and omnivores (2%). Temperate marine herbivorous fish belong to the families Mugilidae, Kyphosidae, Sparidae, Aplodactylidae, Pomacentridae, Odacidae, Stichaeidae, Blenniidae and Monocanthidae. These are cosmopolitan in distribution, with the exception of Aplodactylids and Odacids which are confined to the southern hemisphere (Clements, 1985). Eight New Zealand species of fish are predominantly or exclusively herbivorous (Meekan, 1986). These are the black angelfish *Parma alboscapularis,* parore *Girella*

tricuspidata, bluefish *Girella cyanea*, silver drummer *Kyphosus sydneyanus*, marblefish *Aplodactylus arctidens*, notch-head marblefish *Aplodactylus etheridgi*, blue finned butterfish *Odax cyanoallix*, and the butterfish *Odax pullus*.

Odax pullus is a good species for a dietary study because it adds a new dimension to herbivory in temperate reef fish. Their social organisation is similar to other labroid families, with males in particularly exhibiting phases of high activity (Meekan, 1986; Doak, 1991) which are maintained on an almost exclusive diet of fucoid and laminarian algae (Choat & Clements, 1993). In addition, they are characterised by their internal organisation, with a short gut and an intestinal swelling replacing a true stomach (Clements, 1991). This differs distinctively from other herbivorous fish which usually have longer intestines (Horn, 1992). A special ability to forage mainly on fucoid and laminarian algae, which contain high concentrations of chemical deterrents (Estes & Steinberg, 1988; Gerking, 1994), the presence of a complex gut microflora (Clements, 1991), and the ability to function as active herbivores at high latitudes (Choat & Clements, 1992) indicates that their diet has to be based on a unique pattern of food processing and assimilation.

Choat & Clements (1992) determined that the diet of *Odax pullus* in north-eastern New Zealand is dominated by mature fucoid and laminarian algae, showing clear differences from other temperate water herbivorous fish. Butterfish show distinct preferences for certain parts of specific algae. Choat & Clements (1992) found that *O. pullus* select the receptacles and growing tips of the thalli in *Carpophyllum* species and the secondary laminae bearing the sori in *Ecklonia radiata*. During the reproductive season of fucoid and laminarian algae, *O. pullus* select mainly reproductive tissue.

4.1.2 Dietary selectivity

The phenomenon of selective feeding (electivity) is well known in fish. Tsuda & Bryan (1973) showed that there were distinct preferences for particular algal taxa in the two rabbitfish *Signaus rostratus* and *S. spinus* (Signaidae). *S. spinus* avoided the green

alga *Chlorodesmis fastigrata* whereas *S. rostratus* quickly devoured it. However, *S. pinus* consumed *Polysiphonia* spp., which were rejected by *S. rostratus*. This established that at least some plant-eating reef fish recognise and selectively feed on particular food sources.

Selective feeding depends on a variety of features, of which some, such as preference for one item of the food complex, are characteristics associated with the feeding animal. Others, such as a greater or lesser degree of protection, are entirely the traits of the food object. However, selective feeding can always be considered as a function of several factors operating simultaneously, with a combination of features of the consumer and the food itself (Ivlev, 1961).

To assess the degree of selective feeding it is necessary to know not only the availability of the separate food items found in the intestinal samples, but also the availability of the same elements in the food supply, in the feeding area. Consequently, the analysis of electivity in herbivorous fish necessitates some knowledge of the abundance and distribution of dietary algal species.

The dietary preferences and feeding behaviour of butterfish have been derived from studies investigating populations in the North Island of New Zealand (e.g. Clements 1985; Meekan, 1986; Clements & Bellwood, 1988; Choat & Clements, 1992, Clements & Choat, 1993) and a small study around the Wellington area (Clements 1985). All of these studies done within the warmer waters of the North Island have shown that *O. pullus* feed predominately on the fucoid *Carpophyllum* spp. and the laminarian *E. radiata*, consuming them in approximately the same proportions in which they occur in the feeding areas (Choat & Clements, 1992).

While the diet of *O. pullus* has been established for fish living in the algal-dominated zones of northern New Zealand, the habitats, in which *O. pullus* live in southern New Zealand vary greatly in terms of algal composition and abundance. The colder waters of central and southern New Zealand have different dominant algal species from those of northern New Zealand (Schiel, 1990). While *Ecklonia radiata* is the most abundant

species in the deeper reef zone of northern New Zealand, along the Kaikoura coast the large fucoid *Marginariella boryana* is the most abundant alga in the deeper zones (10 - 20 m). Consequently, butterfish assemblages around the Kaikoura Peninsula may be expected to show considerable differences in diet to that already described for *O. pullus* in northern New Zealand.

Various factors have been identified as possible causes of differences in food selectivity. Some studies have investigated the influence of algal secondary metabolites on food choice (e.g. Wylie & Paul, 1988; Ireland & Horn, 1991), whereas others have focussed on the food quality of the algae itself (e.g. Neighbors & Horn, 1991) or the nutritional requirements of the fish (e.g. Fishelson *et al.*, 1987). Other workers, such as Horn & Neighbors (1984) and Clements & Choat (1993) have examined the role of ontogenetic and seasonal factors in relation to dietary selectivity.

Dietary selectivity can be caused by variations in diet composition at different developmental stages of fish. Some herbivorous fish undergo an initial carnivorous phase before switching to partial or total herbivory as adults. Barton (1982) showed that young specimens of the monkeyface prickleback *Cebidichthys violaceus* are primarily carnivorous, while older fish are mainly herbivorous. This dietary change is accompanied by an elongation of the gut. Similar changes in diet, corresponding with increased gut length have also been reported for the prickleback *Xiphister mucosus* (Horn *et al.*, 1982). Miller (1975) showed that gut length can change in response to experimental manipulation of the diet. It was therefore suggested that morphological changes may improve the digestive efficiency of the individual, in order to maximise the nutritional value of each food source.

Fish are known to forage selectively on algae with different nutritional values. Fishelson *et al.* (1987) showed that the diet of surgeonfish *Acanthurus nigrofuscus* changes seasonally between different species of algae. The diet changes from very small brown and red algae in the summer to larger brown algae in the winter. Feeding on small particles required prolonged feeding activity and thus higher energy expenditure. Therefore, the switch to larger, more fleshy algae during the colder

months provided more food per unit effort. It was concluded that the rich winter diet provided the energy base needed for gonad development and gametogenesis, whereas the summer diet provided sufficient energy for survival, maintenance and motor activity. However, no indication was given as to whether these dietary changes were exhibited within all age groups of *A. nigrofuscus*.

Variations in the diet of different age groups or sexes are often linked to different nutritional requirements. Many families of herbivorous fish have a carnivorous juvenile phase. These taxa include stichaeids (Montgomery, 1977), girellids (Bell *et al.*, 1980), kyphosids (Rimmer, 1986) and scarids (Bellwood, 1988). The protein content of animal prey is consistently high enough to support growth rates proportional to energy intake. In contrast, the protein content of plant material is usually very low, sometimes below the maintenance level for herbivores (Boyd & Goodyear, 1971). The ontogenetic dietary difference is therefore believed to be partly due to the increased amount of protein necessary to ensure rapid growth of juveniles (Horn, 1989).

Dietary changes may also be related to the morphological and physiological ability to process different dietary items at different developmental stages. Chao & Musick (1977) suggested that intraspecific dietary differences of sciaenid fishes were caused by morphological limitations rather than selective feeding. Stoner & Livingston (1984) found similar results for the spottail pinfish *Diplodus holbroki*, which possessed a small gape and mouth size. Consequently, juveniles were unable to capture large prey such as shrimp, isopods or larger amphipods.

While most studies investigating ontogenetic changes in diet have focussed on feeding morphology and head shape parameters, Otten (1983) demonstrated eye size to be a major factor influencing feeding ability. He showed that, in addition to the importance of absolute eye size for visual acuity, the scale effects of relative eye size and relative adductor mandibulae size are opposite. Therefore, proportionately larger eyes in small fish maximise visual acuity, with the compromise of decreasing bite power (Clements, 1985). Consequently, in the case of herbivorous fish, older individuals are more capable of feeding on tough algal material.

Intraspecific dietary shift from small, soft algal tissue to larger, more fleshy algae may also be related to variations in the depth distribution of different age groups. Habitats are known to differ between depths (see Chapter 2). Choat & Schiel (1982) showed distinct differences in algal abundance and assemblage composition between depths in the subtidal habitats of northern New Zealand. Therefore, differences in the depth distribution of the different ontogenetic stages may affect variations in diet.

The aim of this chapter was to identify the diet of *Odax pullus* populations occupying habitats along the northeast coast of the South Island of New Zealand. This diet could then be compared to the known diet of populations of O. *pullus* in northern New Zealand. An additional focus of this study was the identification of the effect of seasonal differences in algal abundance and ontogenetic changes in individuals on their diet.

4.2 Material and methods

The stomach contents of 302 *Odaxpullus* were analysed. The fish were obtained and handled as described in the previous chapter (section 3.2.). All nets were set in depths between one and six metres. Because of the habitat observations obtained from the habitat description in Chapter 1, the subtidal habitats and biota were known not to differ greatly between sampling sites with similar depth. Due to the similarity of the algal abundance and diversity within shallow sites, the use of different sites as sampling areas was not believed to influence the gut contents results used for the feeding study (Clements, 1985). All specimens were handled with care because O. *pullus* are very susceptible to excretion of their gut contents during capture. All fish were processed as soon as possible after capture in order to maintain the conditions of the internal organs and gut contents. The contents of the intestinal swelling of each fish were removed and placed on absorbent paper to remove excess fluid. The gut contents were then preserved in 10% ethanol.

Before analysis of the gut samples, a pilot study was done to establish possible food categories. Different species of common algae were collected and used as voucher specimens. The material was used as reference material to identify the algal fragments found in the gut samples by superficial examination (Choat & Clements, 1992). All collected algae were stored in 10% ethanol in order to simulate possible effects of the preservative on the colour or consistency of the algal fragments in the gut samples. Animal matter found in the stomach samples was identified using Morton & Miller (1968) and Storch & Welsch (1991). Less common food categories were grouped to obtain ten food categories in total (Table 4.1). Clements (1985) found that this number of categories balanced between the loss of information (by too few categories) and difficulty in the interpretation of results (by too many categories).

For the analysis, each gut sample was placed in a 750-ml glass jar and the volume of liquid was made up to 700 ml with sea water. The jar was then sealed, shaken to prevent stratification and immediately poured into a plastic tray, which had a graticule with a 100-point (10 x 10 cm) grid attached to the bottom. Four random transects (10 cm) were established and all particles that touched a transect line were transferred into petri-dishes. These sub-samples were then examined under a dissecting microscope and the number of fragments of each food category per transect was recorded as a proportion of total fragments. The proportional data were transformed into percentages to eliminate the effects of varying stomach volume, which was mainly caused by the size of the fish and stress-defecation during capture. The mean of the four transects was then calculated, giving an estimate of the relative proportion of each of the ten dietary categories that was ingested by each fish.

Table 4.1 Ten food categories used for the analysis of the stomach contents of *Odax pullus*

Species Name	Code	Included species and algal parts
Lessonia variegata	LES	*L. variegata*
Macrocystis pyrifera	MC	*M. pyrifera* reproductive parts
Epiphytes	EPY	
Marginariella boryana	MG	*M. boryana* reproductive parts
Carpophyllum spp.	CP	*C. maschalocarpum* and *C. flexuosum*
	CPR	*Carpophyllum* spp. reproductive parts
Ecklonia radiata	EK	*E. radiata* reproductive parts
Red seaweeds	RS	mainly *Polysiphonia* spp.
Animal matter	AM	salps (*Salpa democratica*), sponges, polychaetes, amphipods, fish eggs, shell fragments of snails and bivalves
Other	O	*Landsburgia quercifolia*, *Cystophora torulosa*, *C. torulosa* reproductive parts

The data for all 302 fish were subjected to principal component analysis using a covariance matrix. This identified new axes (Principal components) that summarised the multivariate information of the data set in the best possible way (Dunn & Everitt, 1982). The object of this is to analyse a number of variables and determine combinations of these to produce indices that are uncorrelated (Manly, 1986). According to Clements & Choat (1993), "each axis represents a combination of the original variables and summarises as much of the total variation as possible, subject to the constraint of being independent of the preceding axes". The amount of variation accounted for by each axis is measured by its eigenvalue. These variables are ordered, with the first displaying the largest amount of variation (Daultrey, 1976). The actual variation in the data set can then be adequately described by a few variables with variances that are not significant (Manly, 1986). These can then be used in univariate analyses as summaries of the old variables (Clements & Choat, 1993). Vector scores from the principal component analysis were then used in analysis of

variance (ANOVA) to determine the effects of fish size and season on the diet of *Odax pullus*. The unbalanced nature of the data, however, required that the two-factor design (three size classes, five seasons) was performed on random subsamples, in order to balance the cell counts.

The 302 fish were grouped into three size classes of 0 - 249 mm, 250 - 299 mm and 300 - 400 mm. The unequal size intervals were chosen because of the relatively small sample size of fishes <250 mm and >300 mm. Because of the small sample size of some size classes in individual months, the data were then pooled into seasons:

Summer 1997	(January 1997	→	February 1997)
Autumn	(March 1997	→	May 1997)
Winter	(June 1997	→	August 1997)
Spring	(September 1997	→	November 1997)
Summer 1998	(December 1997	→	February 1998)

4.3 Results

When the data from all stomach samples were pooled by food category, it was found that *Lessonia variegata* appeared to occur at a higher percentage in the stomach samples than any other food category (Figure 4.1). *Macrocystis pyrifera, Marginariella boryana* and *Carpophyllum* made up smaller percentages of the diet. Combining both the categories of *Carpophyllum* makes this species the third most frequent species. Food categories that accounted for less than 2% of the total occurrence was not included in further analyses.

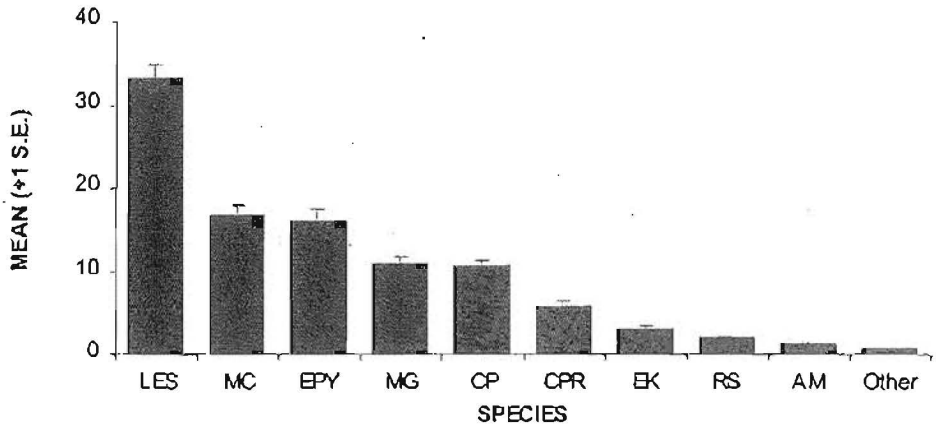


Figure 4.1 Mean percentage occurrence (+ 1 S.E.) of food categories in stomach samples. For species codes see Table 4.1

The first five principal components (PCs) accounted for 71.9% of the total variation in the data set. Therefore, the remaining principal components were only of relatively minor importance and not used in further analysis. The eigenvalues and explained variances of the first five principal components extracted from the covariance matrix of the nine remaining dietary variables are shown in Table 4.2

The first principal component accounted for 18.8% of the variance in the proportions of the nine food categories. This PC primarily represented a trend in the amount of reproductive receptacles of *Carpophyllum* spp. found in the stomach samples. ANOVA showed no differences between the different size classes of fish ($F_{2,105} = 0.85$, $p = 0.43$) and this was constant through time ($F_{2,105} = 0.81$, $p = 0.51$). PC 1 varied between seasons ($F_{4,105} = 8.34$, $p < 0.001$). Tukey's HSD test showed that PC 1 was significantly smaller in spring and summer 1998 than during the summer 1997 ($p < 0.01$) (Figure 4.2).

The second PC, which explained 14.8% of the total variation in the data set, primarily represented a trend in the amount of epiphytes in the gut samples. Similar to principal component 1, all size classes showed similar patterns ($F_{2,108} = 1.73$, $p = 0.18$) and this was constant through time ($F_{2,105} = 0.88$, $p = 0.42$). However, PC 2 varied significantly between seasons ($F_{4,105} = 9.33$, $p < 0.001$) and was considerably smaller in spring (Tukey HSD, $p < 0.01$) (Figure 4.2).

The third PC accounted for 13.62% of the variance in the dietary data, reflecting a trend in the amount of *Macrocystis pyrifera* in the gut samples. In contrast to PC 1 and PC 2, this principal component did not differ between seasons ($F_{4,105} = 1.77$, $p = 0.42$) but showed significant differences between size classes ($F_{2,105} = 7.16$, $p < 0.01$). This trend was constant through time ($F_{8,105} = 0.76$, $p = 0.64$). Tukey's HSD test showed that PC 3 varied significantly among the 250 - 299 mm and 300 - 400 mm size classes ($p < 0.001$).

The fourth principal component accounted for 12.6% of the variance in the data set. It reflected a trend in the amount of *E. radiata* in the diet. The analysis of variance showed no differences between the different size classes of fish ($F_{2,105} = 0.85$, $p = 0.91$), but PC 4 varied significantly between seasons ($F_{4,105} = 2.66$, $p < 0.05$). This trend was constant through time ($F_{8,105} = 0.62$, $p = 0.83$). Tukey's HSD test showed that PC 4 was significantly smaller in winter and spring 1998 than during the summer 1997 ($p < 0.05$).

The fifth PC accounted for 12.11% of the variance in the dietary data, reflecting a trend in the amount of *M. boryana* in the gut samples. Similar to principal component 3, PC 5 did not differ between seasons ($F_{4,105} = 1.64$, $p = 0.17$) but showed significant differences between size classes ($F_{2,105} = 3.22$, $p < 0.05$). This trend was constant between seasons ($F_{8,105} = 0.55$, $p = 0.82$). Tukey's HSD test showed that PC 5 varied significantly among the 0 - 249 mm and 250 - 299 mm size classes ($p < 0.05$).

Table 4.2 First five principal components extracted from the covariance matrix of the primary nine dietary food categories (n = 302). The PCs used for the analysis are printed in bold

Food category	PC 1	PC 2	PC 3	PC 4	PC 5
Lessonia variegata	0.32	0.52	0.62	0.14	0.28
Macrocystis pyrifera	0.12	0.16	**-0.96**	0.05	0.08
Epiphytes	0.1	**-0.95**	0.11	0.1	0.11
Marginariella boryana	0.04	0.23	0.08	0.18	**-0.9**
Carpophyllum spp.	-0.51	0.02	0	-0.58	-0.1
Carpophyllum spp. reprod. receptacles	**-0.69**	-0.15	-0.1	0.1	0
Ecklonia radiata	0.21	0.07	0.04	**-0.84**	0.06
Red seaweeds	0.04	0.28	0.11	0.34	0.53
Animal matter	-0.63	0.18	0.09	0.03	0.05
Eigenvalue	1.7	1.3	1.2	1.13	1.1
Percentage of total variance explained	18.8	14.8	13.6	12.5	12.1
Cumulative variance explained	18.8	33.6	47.2	59.8	71.9

The principal component analysis showed that most of the variation in the diet of *Odax pullus* can be explained by variations in the percentage occurrences of five dietary food items: *Carpophyllum* reproductive receptacles, epiphytes, *M. pyrifera*, *E. radiata* and *M. boryana*. The analysis of variance revealed that the dietary composition of *O. pullus* appeared to be influenced by the size of the fish and the season. In light of these results season and fish sizes are delineated in graphical analysis (see Figure. 4.2).

Figure 4.2 shows the ontogenetic trends and seasonal influence on diet. All size classes showed increased consumption of the reproductive receptacles of *Carpophyllum* and epiphytes during spring. *M. boryana* was eaten in similar quantities throughout the year. A similar trend was observed for *M. pyrifera*, but there was a trend for sub-adults to eat more than the other two size classes. *Lessonia variegata* was eaten in similar proportions by each of the size classes, but there appeared to be a general decrease towards spring in the amount eaten.

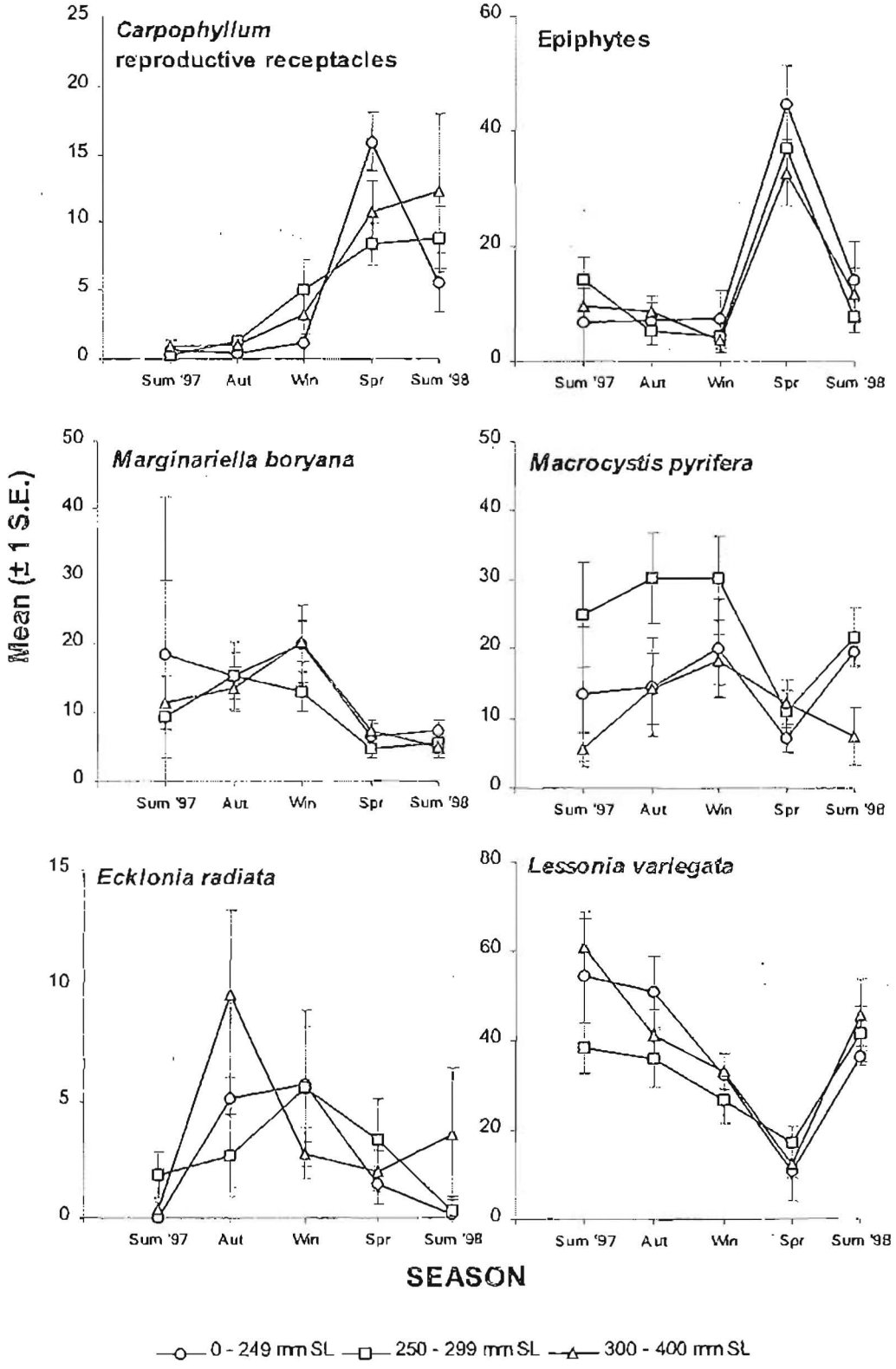


Figure 4.2 Mean percentage occurrence (± 1 S.E.) of six food categories through time within different size classes

Animal matter was found in 68 (22.8%) of the 302 samples of all stomach samples (Figure 4.3).

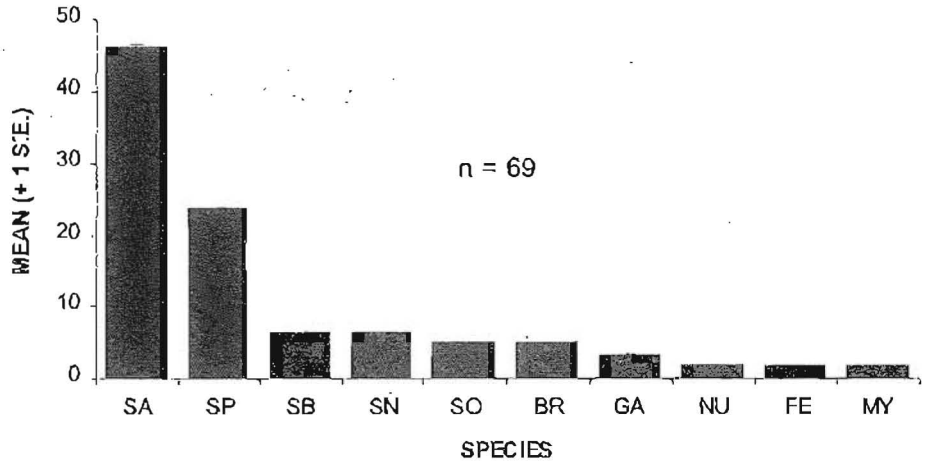


Figure 4.3 Mean percentage occurrence (+ 1 S.E.) of animal matter found in the stomach samples of *Odax pullus* (n = number of samples). Dietary components are graphed by decreasing frequency of occurrence. For category codes see Appendix 1 B

Thaliaceae (salps) and sponge material were found in 44 stomach samples (63.8%) and comprised almost 70% of all animal matter found in the stomach samples. However, the occurrence of salps was highly seasonal, being found only in spring and summer. Salps are most abundant during their reproductive season in spring (Loeb *et al.*, 1997). All other animal material was found in very low quantities throughout the year which indicates accidental ingestion along with algae.

4.4 Discussion

4.4.1 Diet of *Odax pullus*

The results of this study confirm that *Odax pullus* is a true herbivore with a diet composition 98% algal material. The diet is dominated by mature fucoid and laminarian algae, making *O. pullus* very distinct from other temperate water herbivorous fish (Choat & Clements, 1992). Species such as *Aplodactylus arctidens* (Choat & Clements, 1992) and *Parma victoriae* (Jones & Norman, 1986) feed largely on understory algae and the larger perennial species are rarely eaten.

In this study, O. *pullus* showed differences in selection and food preferences to the findings of Choat & Clements (1992). In a study further south in Wellington, Clements (1985) found similar results, with *Lessonia varigata* comprising the bulk of the diet of butterfish caught in the Wellington area. Similar results were shown by Meekan (1986), who investigated the diet of *O. pullus* caught in the Wellington area. The results of this study coupled with those of Clements (1985) and Meekan (1986) suggest a major latitudinal variation in the diet of *Odax pullus*. The stomach contents of fish caught within the Leigh marine reserve were dominated by fucoid algae of the genus *Carpophyllum* and to a lesser extent by *E. radiata.* In this study, however, *Lessonia variegata* was mostly eaten.

The latitudinal differences in *Odax* feeding relate to the differences in algal assemblages found in northern and southern New Zealand. Schiel (1990) showed that *Lessonia variegata,* rather than *E. radiata,* is the major component of the laminarian biomass in the colder waters around the Wellington area. Similar algal abundances have been identified for the habitats around the Kaikoura Peninsula, but *E. radiata* is less frequently seen (see Chapter 2). This latitudinal trend from *Carpophyllum* and E. *radiata* dominated habitats towards increased *Lessonia* abundance is reflected in the diet of *Odaxpullus.* This supports the view stated by Choat & Clements (1992) that the dietary algal species are consumed in approximately the proportions at which they

occur in shallow subtidal habitats. Consequently, *E. radiata* may only be an important component of the diet of butterfish in the warmer subtidal habitats of the North Island.

Dietary choice appears to be strongly influenced by selective feeding of individuals. Within each algal species, *O. pullus* selected particular parts of the algae. Choat & Clements (1992) showed that butterfish actively select the reproductive receptacles of fucoid and laminarian algae during the summer months. This selectiveness also applies to other algal taxa. Species, such as *Landsburgia quercifolia* and *Cystophora torulosa* were shown to occur in the shallow habitats around Kaikoura (Chapter 2). These species were accessible to *O. pullus* but only rarely eaten. Selective feeding is well known in fish. However, for a quantitative appraisal of the degree of selective feeding it is necessary to know not only the ratio between the separate food items, but also the ratio between the same elements in the food complex found within the feeding area.

The results of this study confirm and extend the view of Choat & Clements (1993) and Clements & Choat (1993) that *Odax pullus* feed in a selective manner on a small range of algal taxa. The increased abundance of the reproductive receptacles *Carpophyllum* spp. during spring and summer suggests that this selectivity is extended to specific parts of the algae.

The increased abundance of *Carpophyllum* spp. and their receptacles in the diet may be related to nutritional values. Kaur & Vijayaraghavan (1992) showed that the reproductive parts of fucoid macroalgae contain higher levels of polysaccharides and protein than thallus tissue, thus providing a higher nutritional value. Horn & Neighbors (1984) suggested that the monkeyface prickleback *Cebidichthys violaceus* also fed selectively on the younger distal portions of algae, due to their higher nutritional value. The correspondingly higher amounts of *Carpophyllum* thallus in the gut contents, especially in larger fish, could be explained by the 'incidental' ingestion of thallus material while feeding on reproductive receptacles.

Within the warmer habitats of the North Island, the reproductive receptacles of *Carpophyllum* spp. are believed to be especially important for butterfish in early summer, because levels of the storage polysaccharide laminaran and the sugar alcohol, mannitol, in the laminae of *E. radiata* are low at this time of year (Clements & Choat, 1993). The nutritional importance of these chemicals is made clear by the fact that the feeding of *O. pullus* is usually concentrated on the secondary laminae of *E. radiata* (Clements & Bellwood, 1988). In habitats without *Carpophyllum* spp., however, the congeneric *O. cyanomelas* consume the entire primary lamina and meristem of *E. radiata* (Clements & Choat, 1993). Stewart *et al.* (1961) found that the laminaran content of *E. radiata* increased to a maximum in summer and autumn, coinciding with the highest percentage occurrence of *E. radiata* found in the stomach samples. These findings support the view of Clements & Choat (1993) that the seasonal variation in the storage of polysaccharides and other nutritional components may be an important factor determining the food choice of butterfish.

Dietary selectivity of *Odax pullus* may also be influenced by the avoidance of chemical deterrents produced by some algal species. Targett & Mitsui (1979) showed that toxicity and resulting hemolysis in the red blood cells of the feeding fish are generally found in the three major divisions of marine algae: Chlorophyta, Phaeophyta and Rhodophyta. The effects of polyphloroglucinol phenolics on invertebrate herbivores in algal chemical defenses are well documented in temperate waters (Paul & Fencial, 1986; Hay *et al.*, 1987). Members of the order Fucales and Laminariales in New Zealand typically contain very high levels of polyphenolics (Steinberg, 1989). However, Steinberg (1989) also suggested that the reproductive receptacles of *Carpophyllum* spp. may exhibit lower quantities of the chemical. Therefore, selective feeding on the reproductive tissue may to be interpreted as an attempt to minimise the intake of the chemical, rather than total avoidance.

The analysis of variance on the five principal components showed that differences in dietary preferences were determined by seasonal effects and size of the fish. This is similar to the results found by Clements & Choat (1993). Their study showed that, within the Leigh Marine Reserve, variations in the diet of *O. pullus* appeared to be

size-related. Ontogenetic shifts in the diet composition are a well-known feature in teleost fish (Rimmer, 1986; Bellwood, 1988, Warbuton *et al.*, 1998) and a variety of factors have been identified as possible causes.

Meekan (1986) suggested that juvenile and adult butterfish show different depth preferences. Juveniles are believed to inhabit shallow waters, whereas older fish gradually migrate into deeper waters. Clements & Choat (1993) therefore concluded that the diet may reflect ontogenetic habitat differences. However, their specimens appeared to be collected randomly at various depths. This, in turn, may have allowed bias to be introduced, by only sampling smaller individuals in shallow water. Because of the distinct differences in algal abundances at different depths (Choat & Schiel, 1982), the dietary differences may have been caused by biased sampling rather than by different depth distribution.

Around Kaikoura there is no variation in the depth distribution of different size classes of *O. pullus* (see Chapter 2). However, to eliminate possible site differences, all fish were caught within a depth of 0 - 6 metres. The dietary analysis of the gut samples showed differences between size classes. This is similar to the findings of Clements & Choat (1993) who also found considerable differences in the gut contents of small juveniles and adults. In the present study only four specimens <200 mm were caught. This may explain the lack of a significant result in the size analysis for the 250 - 300 mm and 300 - 400 mm size classes. With respect to the ontogenetic changes, it is possible that sub-adult fish (< 200 mm) have reached a developmental stage that allows feeding on tougher algal species. This appears to be supported by Clements & Choat (1993), who showed that sub-adults (180 - 280 mm SL) and adults (> 280 mm SL) had similar gut contents.

Ontogenetic changes in the diet of *Odax pullus* may also be caused by the morphological and physiological ability to process different dietary items (Clements & Choat, 1993). Butterfish exhibit a variety of morphological changes throughout their life history. Gut length increases very quickly in relation to the total length of the individual. This is a common feature in fish which undergo a dietary shift from

carnivory to herbivory during their early life stages (Montgomery, 1977). The increasing intestinal length is believed to improve the digestive ability by providing a greater gut surface area and increased passage time for the food.

Clements (1985) showed that in butterfish, the proportional increase of intestinal length with size peaked at a standard length between 140 - 150 mm. In specimens above this size the rate of increase was relatively constant. Since the peak may indicate a shift towards an algal dominated diet, juvenile *O. pullus* are believed to include a greater amount of animal matter in their diet (Choat & Clements, 1992).

Animal matter appears to be ingested by all size classes of herbivorous fish. No adult herbivores are obligate algal feeders, selectively excluding all animal food from their diet (Gerking, 1994). However, the increased feeding of juvenile and sub-adult butterfish on animal material, such as gastropods, crustaceans and bryozoans (Clements & Choat, 1993) may be attributed to the increased quantity of protein necessary for the rapid growth of young fish. Lellis & Smith (1992) showed that the amount of muscle, fat and bone, and thus the type and quantity of energy reserves, deposited by juvenile chinook salmon can be dramatically altered by adjusting the protein content of the feed. This increased protein content of the diet may promote developmental growth.

Growth in *Odax pullus* results in marked ontogenetic changes in head shape. Ritchie (1976) showed distinct changes in the snout angle, which increases from about 30° in juveniles to more than 80° in large adults. This was largely caused by an increase in cheek depth (Clements, 1985). The deeper head and therefore increased gape provides a proportionally greater surface area for the attachment of the jaw musculature (Clements & Bellwood, 1988), thus increasing the bite power (Bone & Marshall, 1985). Clements & Choat (1993) concluded that the small intestinal length, combined with a relatively weak jaw apparatus, may prevent small juveniles from feeding on the same algal taxa as adult butterfish.

In conclusion, the dietary composition of *Odax pullus* along the northeast coast of the South Island differs considerably from their North Island counterparts. This supports the results of Clements & Choat (1993) that the diet reflects the algal abundance of the habitat. Further investigations showed that diet of butterfish around the Kaikoura Peninsula appears to be influenced by season and by size. However, this may only apply to individuals ranging from sub-adults to adults. Further investigations into the feeding of juvenile *O. pullus* are therefore necessary to determine the importance of size on the diet of early life history stages.

CHAPTER FIVE

Behaviour

5.1 Introduction

In order to extend knowledge about the ecology, life history and social structure of an animal, it is necessary to gain a better understanding of its behaviour and time budget (Apfelbach & Döhl, 1980). The literature provides only sketchy information on the behaviour of *Odax pullus*. Most of this information involves movement patterns related to feeding (Clements & Choat, 1993; Choat & Clements, 1993).

Marine teleosts show a variety of behaviours. There have been few behavioural studies done on temperate marine species, providing only very limited information on the behaviour of fishes in habitats other then coral reefs. Especially in labroid species, these behaviours are many and varied and can be grouped into categories, such as locomotion, feeding and territorial behaviour (Roede, 1972).

5.1.1 Locomotion

Marine fish species can be divided into specialists and generalists with respect to their swimming ability (Webb, 1984 a,b; Videler, 1993). Within the specialist group a further grouping is apparent. Some species are well adapted for cruising (pelagic sharks, tuna, mackerel) or manoeuvring (coral reef fish, butterflyfishes), while others are specialists for accelerating (barracudas). Generalist swimmers have developed body forms that allow a reasonably good performance in all of the special functions (e.g. salmonids, labrids) (Videler, 1993).

Because of the similarities in body and fin shape in most labroid species, *Odax pullus* could be considered a generalist swimmer. Similar to labrids (Roede, 1972), butterfish possess the ability to manoeuvre accurately with the help of their pectoral fins and are capable of fast movements by tail oscillation. The degree of effectiveness of the fin movements depends on the shape and size of the body (Bone & Marshall, 1985). Therefore, the distinct changes in body-shape during the life history of *O. pullus* (see

Chapter 1) may result in variation in the locomotive behaviour between ontogenetic stages.

5.1.2 Feeding

The common view of a herbivorous animal that feeds exclusively on plants cannot be applied to fish without some limitations. Herbivory in marine fish must be regarded as a relative rather than an absolute term (Clements, 1985). Regardless of the feeding method and dietary choice of their adult counterparts, most fish larvae are visual, raptorial planktivores (Hunter, 1981; Govoni *et al.*, 1986). Usually within the first year of their life, however, herbivorous species shift to an algae-dominated diet (Gerking, 1994). This diet usually also includes animal material. According to Gerking (1994), no herbivorous fishes selectively exclude animal matter from their diet. Herbivorous fish which ingest animal material can be divided into two basic groups. Species belonging to the first group do not appear to target animal prey actively, but some invertebrates associated with algae may be ingested incidentally. The second group contains species that show opportunistic carnivorous tendencies. Fish belonging to this group feed predominately on algae but also take smaller invertebrates when they are encountered.

Clements (1985) categorised *O. pullus* as a facultative herbivore which also selectively takes animal material. This was based entirely on analyses of stomach samples. The amphipod *Amphiroidea falcifer*, which was found in relatively high numbers in stomach samples, usually inhabits the interstices of *E. radiata* laminae. Since the feeding of butterfish in the northern parts of the North Island is concentrated around secondary laminae bearing sori (Choat & Clements, 1992) and butterfish were never observed to target *A. falcifer* while feeding, it was not believed that *A. falcifer* had been ingested incidentally on such a frequent basis.

5.1.3 Territorial behaviour

Apart from reproduction, many fish species are likely to engage in other social behaviour, both affiliative and agonistic (Colgan, 1993). Social behaviour may involve other species, in particular during territorial behaviour (Stevens & Zerba, 1981) or interspecific shoaling (Ehrlich & Ehrlich, 1973). According to Colgan (1993), aggressive interactions, as with courtship behaviour, are the result of internal and external factors such as hormone activation or territorial conflicts.

Aggressive behaviour and displays caused by territorial conflicts are common features in marine fish, especially in labroid species. Territorial agonism can be for any defended area (Mater & Lott, 1995) and is usually caused by competition for a limited resource such as shelter, food, spawning, nest sites or mates (Ross; 1990, Helfman *et al.*, 1997). An individual will defend its territory only if the benefits, such as an increased foraging efficiency (Brawley & Adey, 1977), a lower predation risk (Symons, 1974), increased mating success (Gross, 1991) and offspring survival (Perrone, 1978), exceed the cost. The costs usually include an increased risk of injury (Enquist *et al.*, 1990) or the increased amount of energy spent during defence activity (Hinde, 1973; Puckett & Dill, 1985; Grant, 1997). Aggressive behaviour is generally limited to displays rather than actual fights which could result in injury or death (Siewing, 1980). In labroid species, imposing displays are very common and can be observed as rapid swimming motion combined with raising of the dorsal fin.

5.1.4 Shoaling

Some studies have mentioned the formation of groups of *O. pullus* (e.g. Meekan, 1986). Congregations can provide fish with many advantages, mostly concerning predation and food supply. Predators and food, therefore, are the proximal keys for understanding of fish congregations (Pitcher, 1993). This applies even though the actions and behavioural patterns of the individuals may not be mutually coordinated and organised (Radakov, 1973). The lack of coordination of activity in some groups

compared to the strict organisation in others necessitates definitions for each type of assemblage. According to Pitcher (1993) synchronised and polarised groups are termed *schools*, whereas congregations of fish arising and remaining for social reasons are called *shoals* (Kennedy & Pitcher, 1975). This latter term is comparable to 'flock' for birds, which has no implication for structure or function but rather defines a social form of grouping. According to Breder (1959), a further sub-definition has to be taken into account which divides 'facultative' and 'obligate' grouping behaviour. Obligate grouping occurs is found in species that usually congregate, whereas facultative grouping is usually found in mixed species assemblages that form only infrequently. Schooling and shoaling, however, are not necessarily mutually exclusive, because of their similarities in behavioural patterns and responses. In some instances one form of grouping may change to the other. Shoals that travel, for example, may temporarily show schooling behaviour owing to the developing polarity and synchrony of the individuals.

The forming of fish shoals can be attributed to a variety of reasons. It is possible that advantageous conditions for a species arise simply as a result of being together, independently of behaviour (Radakov, 1973). For example, Tsuneki and Sasaki (1957, cited in Radakov, 1973) found that the ricefish *Oryzias latipes* showed higher tolerance levels to harmful substances in the water when individuals were held together. However, regardless of behaviour, one important advantage of congregating is protection from predators.

Shoal assemblages are believed to improve predator avoidance, thus increasing the chance of survival for the individual. According to Pitcher (1993) grouping may decrease the number of predator-prey encounters, since the travelling predator is less likely to enter the detection range of a group than encounter one of the many ranges of scattered fish. This is because the frequency of predator-prey encounters is an inverse function of the number of shoaled prey (Keenleyside, 1979). Brock & Riffenberg (1960) and Taylor (1984) suggested that, because all individuals are congregated in one area, the predator may not encounter the individuals during a search. If the shoal is regularly missed, the lower number of prey encounters per

search effort could eventually lead to the predator leaving the area. Treisman (1975), however, pointed out that predation pressure may only be reduced if the predator can eat at only one individual or a small proportion of the group, thus allowing the escape of the others and reformation of the shoal.

The aim of this chapter was to investigate three aspects of the behaviour of *O. pullus*. First, the major behavioural patterns and the amount of time allocated to them were identified. These results were then compared between the different ontogenetic stages of butterfish. The second section of this chapter identified patterns of social interactions of *O. pullus* with conspecifics and other species. The third section investigated the feeding behaviour of *O. pullus* with respect to ingested animal material. An attempt was made to identify whether animal matter was actively targeted or only ingested incidentally.

5.2 Materials and methods

Observation on the activity patterns and feeding behaviour of *Odax pullus* was done at several sites around the Kaikoura Peninsula (Plate 5.1). The sites were chosen because of their suitability for behavioural observations in terms of butterfish abundance, depth and water clarity. Preliminary dives were carried out to determine sites with a high abundance of *O. pullus* at a depth less than five metres where underwater visibility tends to be greatest.

The behavioural study had two parts. The first investigated the time-budget of butterfish and a second set of observations focussed on behavioural events that did not occur frequently. All observations were carried out using snorkel equipment. Observations on SCUBA were not done because of the possible behavioural changes caused by noise and turbulence due to air-bubbles (see Chapter 2).

Plate 5.1 Aerial view of the Kaikoura Peninsula. Study sites are marked with white arrows

For the 'time-budget' study, data were collected by following randomly selected individuals. Each fish was followed for a brief period without recording, so that the fish became accustomed to the presence of the diver. Prior to the first recording, the sex, colouration and size (SL) to the nearest centimetre were recorded. Thereafter, recording commenced and the behavioural actions were recorded every 10 seconds on a preformatted plastic slate. This time span provided a good compromise between the amount of time needed to record the last action and an actual change in the behaviour of the fish. The term 'run' used by Clements (1985), describing the sequence of minutes of each observation, was adopted. Runs were discarded if the individual was not kept in view for longer than 60 seconds. Although Choat & Clements (1993) discarded observational runs shorter than three minutes, the 60 seconds used in this study represented a good compromise between the loss of information due to time shortage and losing sight of the fish caused by poor visibility and complex habitat structure.

Preliminary observations were carried out before the behavioural studies began. All observations were grouped into the three main categories of swimming, feeding and other behavioural actions. The specific types of behaviours and their descriptions included in these categories are shown in Table 5.1.

Table 5.1 Behavioural categories and sub-categories used for the observation of the time-budget- study for *O. pullus*. Swimming modes adopted from Keenleyside (1979)

Behaviour	Sub-category	Description
Swimming	Swimming slow (SS)	Very slow movement, forward thrust only with the help of pectoral fins, movement above substratum (labriform mode)
	Swimming fast (SF)	Medium to fast swimming speed, forward thrust generated by tail oscillation, movement above substratum (subcarangi-form mode)
	Swimming in weed (SW)	Slow and fast movement combined, movement within the seaweed
	Hovering (H)	No movement, pectoral fins used only for balance
	Hovering in weed (HW)	No forward movement, fish remains motionless within the seaweed
Feeding	—	Feeding on algal and animal material
Other	All behaviours other than the two above	intraspecific and interspecific behaviour

To test the effects of the size on the swimming behaviour, all observed fish were grouped into size classes of 5 -15 cm, 16-25 cm, 26-35 cm and 36-50 cm. The unequal size intervals were chosen because of the relatively small sample size of fishes <100 mm and >400 mm. The data were first transformed into percentage values to remove the effects of the varying duration of each observation period and then analysed using a one-way analysis of variance (ANOVA).

To determine temporal differences in the feeding activity of *O. pullus*, all observations were grouped by time of the day, using five time periods: dawn (sunrise - 0800), morning (0800 - 1200), noon (1200 - 1500), afternoon (1500 - 1900), dusk (1900 - sunset).

The detailed study of 'other' behaviours (Table 5.1) involved the observation of single individuals or groups of *O. pullus*. All individuals were observed for as long as possible. Instead of recording every ten seconds, all behavioural actions other than swimming and feeding were recorded and described when they occurred. The behaviour was first assigned to a specific category and then described in detail (see Table 5.2).

5.3 Results

5.3.1 Time Budget

During the 'time-budget' study 287 fish were observed with a total observation time of 9.1 hours. *Odax pullus* spent most of their time either swimming or feeding, whereas interactions were seldomly seen. There were no differences in the amount of time spent on swimming ($F_{3,172} = 2.55$, $p = 0.06$) or feeding ($F_{3,172} = 2.63$, $p = 0.05$) between different size classes (Figure 5.1).

Within the swimming patterns it appeared that there were differences between the different size classes. Individuals in the smallest size class (5 - 15 cm) spent more time swimming in a slow motion and hovering than fish in the largest size class (36 - 50 cm). In contrast, larger individuals showed more rapid swimming motions and sought more shelter within the seaweed (Fig. 5.2).

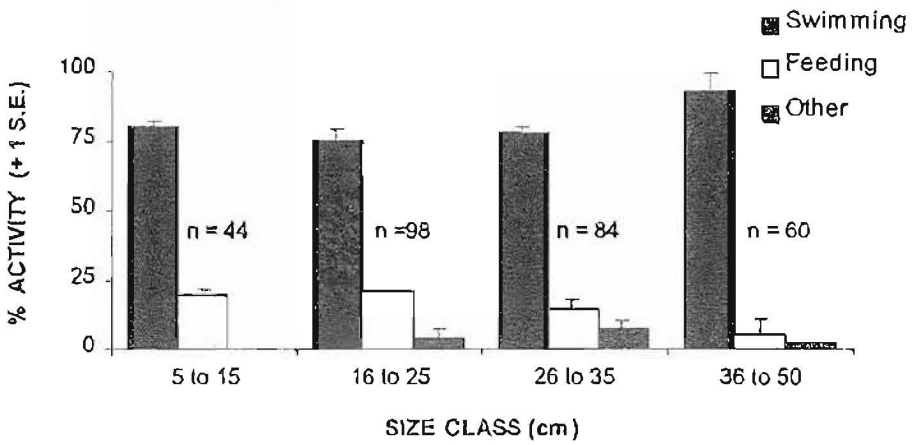


Figure 5.1 Activity patterns (Time Budget) of *O. pullus*
(n = number of fish observed)

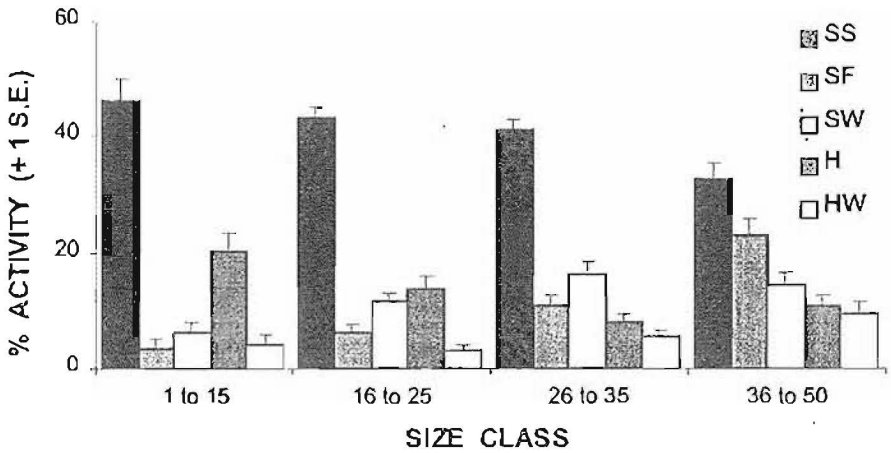


Figure 5.2 Mean percentage activity of different *O. pullus* size classes.
For legend codes see Table 5.1

The feeding activity of *O. pullus* varied between different times of the day ($F_{4,171} = 4.26$, $p < 0.01$) (Fig. 5.3). There was a gradual decrease in feeding activity from dawn towards noon. There was a peak in feeding activity in the afternoon, when fish actively fed for 26% of the time, followed by less activity in the evening (after 7 p.m.).

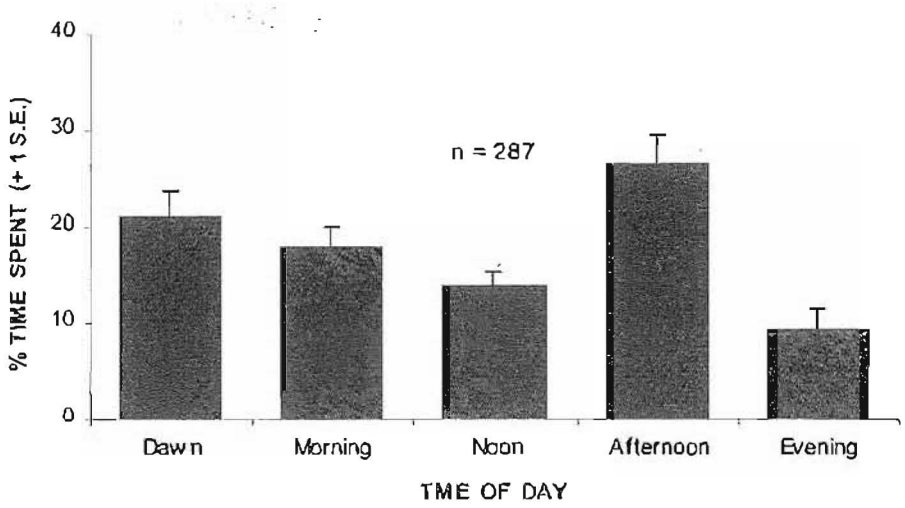


Figure 5.3 Mean percentage feeding activity of *O. pullus* throughout the day (n = number of fish observed)

5.3.2 Interactions

This part of the study involved the observation of 186 fish (Table 5.2). With the exception of shoaling, which occurred in one third of all the fish observed, butterfish showed few inter- and intraspecific interactions. Some species such as *Notolabrus celidotus*, *Notolabrus fucicola* and *Aplodactylus arctidens* were observed chasing individual *O. pullus* over various distances. *A. arctidens* usually drove butterfish only out of their immediate vicinity, whereas a chase by *N. celidotus* and *N. fucicola* sometimes continued over several metres. Chasing of conspecifics was observed only in two out of the 473 butterfish observed in the entire study. These chases did not continue for more than one metre.

Table 5.2 Infrequent behaviour patterns of *O. pullus* and the total number of fish observed in each category

Behaviour	actions involved	No of times obs.
Interspecific interactions	- butterfish are chased by other species, such as *N. celidotus*, *N. fucicola* and *A. arctidens*	7
	- schoaling with blue moki *L. ciliaris*	11
Intraspecific interactions	- chase	2
	- swimming or hovering in very close proximity to conspecifics	62
'Unusual' feeding behaviour	- feeding on salps, actively targeting the stomach	49
	- feeding on polychaetes: sucking in of the prey may be followed by expectoration	21
	- intensive examination of food material (> 10 s)	7
	-'scrap-picking', feeding on material stirred up by other fish	9

Shoaling was a common behaviour observed during this study. Interspecific shoaling made up 6% of all behaviours recorded and involved the temporary association of *O. pullus* with blue moki, *L. ciliaris*. The moki shoals usually consisted of approximately 20 - 40 individuals of a wide range of sizes. During each observation about 2 - 3 butterfish were integrated into the shoal in the water column at approximately 3 - 4 m depths. Although it was not observed if butterfish actively swam into the shoal, all observed individuals appeared to follow the movements of the aggregation, even during flight reactions. During the time observed, individual *O. pullus* appeared to maintain a relatively constant central position within the shoal.

Intraspecific shoaling of butterfish was recorded in one third of all individuals observed. Sometimes up to 10 individuals were seen swimming or hovering in very close proximity to each other. Within each of the assemblages observed, some

individuals were seen to feed while others hovered, maintaining their relative position in the shoal. If the shoal was disturbed, individuals usually showed two successive reactions, depending on the degree of the disturbance. If seals were present, the assemblages became very compact. If a seal came too close, individuals either scattered or fled jointly in the same direction.

5.3.3 Feeding

Many butterfish were seen actively feeding on at least two types of animals, the chain salp *Salpa democratia* and the scaleworm *Lepidonotus polychroma*. When feeding on salps in the water column, the fish used two or three bites in rapid succession to tear a hole in the tunica to expose the stomach, which was then ingested. In some cases the stomach was expectorated and body material that was still attached was carefully removed with several bites. While feeding on floating polychaetes, each individual carefully observed the animal from a very short distance for several seconds. After initial ingestion, the prey was sometimes expectorated and re-ingested. This process was often repeated several times. During other observations some butterfish fed on the material stirred up by foraging blue moki but it was not possible to determine whether the ingested material consisted of algal or animal matter.

5.4 Discussion

This study shows that *Odax pullus* display a wide variety of behavioural patterns, similar to those seen in labrids. The time allocated to each behaviour greatly differs between the behavioural categories. The large amount of time spent on swimming and feeding appears to confirm the results of Choat & Clements (1993) that butterfish are very active fish. However, this study showed that different size classes have considerable differences in swimming activity thus contradicting the view that all *O. pullus* exhibit continuous swimming behaviour (Choat & Clements, 1993). The differences in the swimming behaviour between the different developmental stages

of butterfish may be directly related to energy expenditure, reproduction, feeding and escape from predators.

The cost of swimming can be expressed as the sum of the standard metabolic rate and the energy needed to produce thrust, to accelerate and to overcome the drag forces (Bone & Marshall, 1985). The cost increases with speed but this depends on the species, size, water temperature and the condition of the fish (Videler, 1993). In sharks of the family *Scyliorhinidae*, for instance, a doubling in swimming speed results in an eight-fold increase of energy expenditure (Bone & Marshall 1985). Differences in the swimming behaviour may, therefore, be affected by the various developmental stages of *Odax pullus*.

Small fish experience viscous drag as a major force (Wootton, 1992); the smaller the fish the shorter the gliding distance will be after locomotion stops (Webb & Weihs, 1986). Because of this larger individuals are able to glide forward through the water at the end of a period of active propulsion, thus allowing for longer intervals between tail oscillations. This, in turn, reduces the energy used, which is necessary if longer distances have to be covered.

The increased mobility and therefore greater distance covered, may also be related to territorial behaviour. During the reproductive season (July - January, see Chapter 3) male butterfish are believed to establish loose territories (Ritchie, 1969). Maintaining and patrolling these territories could be one possible explanation for the increased activity of male *O. pullus*. Other factors, however, such as flight response, may also contribute to this increased activity.

Flight reaction in fish is not stereotypical and differs considerably between species, involving cover seeking or rapid swimming. Older butterfish tend to be more wary of divers (Chapter 2), whereas smaller *O. pullus* do not appear to show any reaction. This ontogenetic change in flight behaviour may be caused by learning (Pitcher, 1993). Magurran (1990) showed that in minnows the various types of predator avoidance were significantly enhanced in fish that had experienced previous predatory

attacks. Similar results were shown for coho salmon juveniles that had been exposed to simulated predator attacks and, subsequently, showed a higher survival rate in real attacks than 'untrained' fish (Olla & Davis, 1989). During their life history, butterfish may experience events such as an actual attack by a predator, the entanglement in a gill-net or wounds inflicted by a spear gun. These events may be comparable to the narrow escape from a predator attack and could result in increased awareness of those individuals to a predator.

Increased awareness and flight behaviour may also be related to the minimal approach distance. It has been shown that many fish species attempt to keep a minimum distance of at least 15 body lengths between themselves and a predator (Pitcher & Wyche, 1983; Magurran & Pitcher, 1987). This is believed to maximise an advantage in relative manoeuvrability and acceleration for the individual (Weihs & Webb, 1983). Smaller butterfish may appear to be more approachable than adults. This could be regarded as increased awareness of older fish, though, juveniles and adults probably keep similar flight distance in relation to their body size.

Ontogenetic changes in colouration may also contribute to the increased mobility of adult *O. pullus*. Camouflage using countershading is a common feature in fish that swim close to the water surface or inhabit shallow well-lit areas (Bone & Marshall, 1985). During their life history butterfish undergo extensive colour changes; the light colouration of juveniles darkening with increasing age and size (Chapter 1). Large adults are characterised by a very dark dorsal region (melanophores) and a light ventral side (guanine). According to Doak (1991), these colour patterns enable them to evade predators by swimming low over the kelp canopy rather than hiding among the fronds like juvenile butterfish.

The decreased swimming activity and hiding of juvenile *O. pullus* could be related to increased energy requirements due to growth. Koch & Wieser (1983) postulated that fish may show a trade-off between swimming activity and the production of gonads or ontogenetic development. In the roach *Rutilus rutilus*, for example swimming activity

was reduced during the synthesis of the reproductive system, whereas outside the reproductive season individual movement increased considerably.

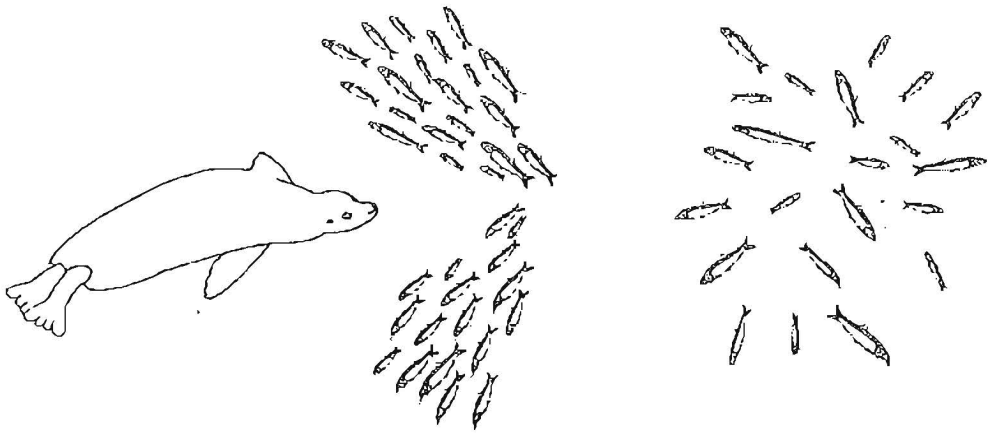
Although the daylight activity of *Odax pullus* is dominated by feeding and swimming, butterfish also display some intraspecific and interspecific interactions, although they were uncommon. In these observations, however, *O. pullus* never initiated an interspecific confrontation or responded in any other way than flight, thus minimising agonistic behaviour. A reduction of agonistic behaviour can be attributed to differences in diet among co-inhabitants. According to Thresher (1979) interspecific interactions are usually caused by competition for food sources. Because *O. pullus* are herbivores, they are unlikely to compete with carnivorous species such as *Notolabrus fucicola* or *N. celidotus*. In addition, butterfish do not appear to compete with other herbivorous species such as the marblefish *A. arctidens*. This may be because marblefish forage on smaller, softer red algae while butterfish preferentially feed on large fucoids and laminarians (Choat & Clements, 1992).

Aggressive behaviour (e.g., chasing) is usually related to the territorial behaviour of certain species. According to Colgan (1993) some fish species chase others away from their vicinity wherever they happen to be, whereas others only defend well-defined areas. Border disputes and territorial behaviour usually serve to protect and guard an area suitable for reproduction (Siewing, 1980, Stevens & Zerba, 1981). *O pullus* do not appear to establish territories and therefore do not appear to exhibit border disputes. The only exceptions to this are large males during the reproductive season (Francis, 1988). The absence of territorial behaviour may have been one reason for the forming of intra- and interspecific shoals.

Shoaling butterfish may detect a predator earlier than a single individual. A study on the shoaling behaviour of minnows found that larger congregations had decreased detection times for an approaching predator (Magurran *et al.*, 1985). The New Zealand fur seal *Arctocephalus Forsteri* is the most obvious predator of *O. pullus* (Street, 1964). Although fur seals usually feed several miles offshore, hunting for squid and fish (Wilson, 1974), they often swim inshore, scanning the sea floor for prey, such as

octopus and fish (Stirling, 1970). Fishers who observe seals with prey items on the surface often identify the food as butterfish (pers. communication; Street, 1964). By congregating, fish may, therefore, increase their individual fitness by reducing the detection time of butterfish to a potential predator. A similar advantage has been found for the formation of flocks in birds (Kenward, 1978). In contrast to the reaction patterns of bird flocks, the detection of a predator in fish shoals does not necessarily induce a flight reaction, but is likely to change the behaviour and dynamics of the shoal (Pitcher, 1993).

The dynamics and behavioural responses of butterfish assemblages are likely to be affected by the presence of a predator. Swimming close to conspecifics may increase the vigilance of individuals. Andorfer (1980) showed that shoals of belica, *Leucaspius delineatus*, became more compact and cohesive in the presence of pike. 'Compacting' is believed to enable the members of the assemblage to use advanced cooperative escape techniques, such as splitting or flash expansion (Plate 5.2), followed by a reformation of the group.



A. Split B. Flash expansion

Plate 5.2 Mechanisms of fish assemblages for the avoidance of a predator

The forming of butterfish shoals may also be related to the optimisation of feeding time. The Optimal Foraging Theory predicts rules on how an animal should forage to maximise its fitness (Gerking, 1994). Two basic predictions are that food has to be obtained in the most economical way and predators have to be avoided. Teleost fishes are not usually able to meet those criteria sequentially (i.e. foraging when hungry and avoiding predators when satiated) (Milinski, 1993). Consequently, these interactions often appear to be closely linked, creating a trade-off between the energetic return from feeding activity and the degree of predation risk accepted by the animal.

Feeding and the search for food by *O. pullus* may also benefit from interspecific shoaling. Some labroid species, for example, are known to accompany bottom-feeding fish that root the substratum and feed on stirred-up prey organisms (Randall *et al.*, 1978; M^{c}Cormick, 1995). A similar behaviour is seen in *O. pullus*, which occasionally swim amongst shoals of feeding moki and banded wrasse, searching the stirred-up material for potential food.

The interspecific shoaling behaviour of *O. pullus* with blue moki may yield similar advantages to those gained from congregating with conspecifics (Ehrlich & Ehrlich, 1973). The early recognition of predators may be improved if one species is more vigilant than the other. Blue moki are very vigilant fish (pers. observation) and usually show a flight reaction at the slightest form of disturbance. The temporary association of butterfish with moki may, therefore, enable them to allocate less time scanning the area for predators and more time feeding.

Shoal formation of *O. pullus* may increase the actual feeding time while decreasing the risk of predation. Magurran & Pitcher (1983) showed that individuals within large shoals of cyprinids allocated more time to feeding than fish belonging to smaller congregations. Larger shoals also appear to be more tolerant to an approaching predator, thus increasing the feeding time (Magurran *et al.*, 1985).

This study confirms the supposition of Clements (1985) that there may be an active intake of animal material by butterfish besides the incidental ingestion. The active

targeting of the stomach of salps appears to be similar to the preference for feeding on the reproductive receptacles of *Carpophyllum spp.* (see Chapter 4). However, due to the small proportion of animal material ingested butterfish could be classified as 'herbivores showing occasional omnivory'. Although *O. pullus* display a variety of behaviours predominantly in relation to swimming or feeding, no behavioural patterns related to reproduction were observed. Future studies focussing on twilight activities may clarify the nature of reproductive behaviour such as courtship and spawning. Furthermore, the omnivorous tendencies in relation to herbivory in temperate marine fish appear to warrant more research.

CHAPTER SIX

General Discussion

6.1 Population dynamics

The main objective of this study was to examine the life history features and feeding behaviour of the endemic herbivorous fish *Odax pullus* in a southern temperate reef environment. Butterfish is a ubiquitous species occurring almost around the entire New Zealand coast in shallow areas wherever large brown algae are abundant. However, they do not occur at the Three Kings Islands, off northern New Zealand, where they are replaced by *Odax cyanoallix* (Ayling & Paxton, 1983; Hardy *et al.*, 1987). *O. pullus* is a true cold water species rather than one of subtropical origin that extends its range into southern waters (Choat & Clements, 1992). It is clearly more abundant with increasing latitude and is particularly common from Cook Strait south. Greatest abundances have been recorded from the Chatham Islands and Stewart Island (Schiel unpublished data) and their southern distribution extends to the Snares Islands (Francis, 1996). They do not occur at the sub-antarctic Auckland Islands (Kingsford *et al.*, 1989).

The distinct spatial differences in abundance of *O. pullus* raise the question about the ecological importance and adaptive significance of different life-history traits for the population dynamics of this species. Patterns of changes in abundance and production by a population partly reflect the importance of recruitment, mortality, fecundity, growth and longevity. Although no detailed quantitative data exist on recruit numbers and their site-to-site variation, observations around the Kaikoura region indicate that butterfish recruits are found at least in small numbers during the summer months (pers. observation). Most recruits are seen in shallow algal dominated areas fish < 30 mm are also found to at least 20 m depth. However, in comparison to other abundant reef fish, such as spotties, *O. pullus* around Kaikoura appear to have relatively low recruitment rates. During this study, very high numbers (> 80 per 750 m^2) of newly recruited *Notolabrus celidotus* were seen within shallow habitats (Chapter 2). These high numbers are not a localised phenomenon because Jones (1984 b) showed that recruitment of this species exceeded 250 individuals per 500 m^2 in

shallow algal forests in north-eastern New Zealand. Densities of adult spotties, however, did not exceed 20 individuals, suggesting a relatively high mortality rate between settlement and maturity. The relatively high abundance of adult butterfish observed in relation to the low number of recruits observed could be an indication of high post-recruitment survival or low but regular recruitment, or may merely indicate that small fish are too cryptic to count reliably.

The influence of mortality on the population dynamics of *O. pullus* has not been established but fishing pressure almost certainly has a localised structuring effect. Greatest abundances have been recorded in places with no recent fishing pressure, such as along the Chatham Islands and Stewart Islands. Hickford (1993) and Hickford & Schiel (1995) found that butterfish was the most common species caught in gill-nets around Kaikoura. Using a standard 4.5 inch gill net, fish larger than 270 mm tend to be caught. The relatively small proportion of larger fish found in my study may, therefore, be the result of fishing pressure. However, butterfish populations appear to replenish themselves, which is indicated by fairly stable landing estimates for the commercial catches (Paul, 1997), although there is, anecdotal evidence that butterfish populations in some areas have shown a gradual decrease in the last two decades.

The size frequency distribution of butterfish around Kaikoura shows considerable bias towards fish between 200 - 300 mm SL. This result may be influenced by a sampling artefact because of the tendency to under-sample small cryptic juveniles and highly mobile, wary males. However, the high abundance of medium-sized fish, regular recruitment events and a relative short life expectancy of only 9 - 10 years suggests that butterfish populations have a relatively rapid turnover.

The most abundant inshore reef in New Zealand, *Notolabrus celidotus*, has a similar life span (Jones, 1980). This species, however, has a more rigid social hierarchy than butterfish. Male spotties maintain and defend territories, courting females within them. All large spotties are male, but there are relatively few of these in a population. In

contrast, another common inshore species, *Notolabrus fucicola*, is long-lived probably up to 35, has very low annual recruitment, and apparently large females and males (Denny, 1998).

6.2 Herbivory

Throughout New Zealand, large populations of *O. pullus* are associated with dense beds of macroalgae and this is true around the Kaikoura Peninsula (Chapter 2). These observations stand in contrast to the view that temperate water herbivorous fish are generally 'rare' (Odgen & Lobel, 1978) and that only a very small number of fish use the large biomass of macroalgae in temperate waters as a food resource (Gaines & Lubchenco, 1982). However, Choat (1982) stressed the importance of keeping a clear distinction between species richness and population density in discussing herbivory in temperate waters. The number of species of herbivorous fish declines from the tropics to temperate areas but the local abundance and biomass of one or a few cold temperate species can be high. About 400 reef and reef-associated fish species have been recorded from New Zealand waters (Francis, 1996) but only eight species of the resident fish fauna have a predominantly or exclusively herbivorous diet (Meekan, 1986).

Herbivory in marine fish has received considerable attention in recent years, especially the modes and occurrence of herbivory in tropical waters. Most ecological and physiological questions concerning temperate marine herbivory involve feeding, food choice and digestion (Horn, 1992). Coral reefs appear to have a higher percentage of herbivorous fish than any other single habitat. One estimate is that 50% of coral reef fish are herbivores (Gerking, 1994). The great habitat diversity on coral reefs combined with the high abundance of relatively palatable soft red and green algae may explain why herbivory is more prevalent in tropical waters than in temperate zones.

While the importance of piscine herbivores to subtidal habitats in the tropics has long been acknowledged, the function of herbivorous reef fish in inshore systems is still relatively unexplained. This is especially so in cold temperate areas where herbivory is quite different from the tropics. Tropical fishes, in particular the abundant acanthurids, scarids and siganids, graze mostly on turfs of many species of small filamentous algae. Temperate fish tend to feed selectively on macroscopic algae, including large laminarian and fucalean species (Horn *et al.*, 1982; Horn, 1989; Choat & Clements, 1992).

Herbivorous fish are more diverse in tropical than in temperate waters, and few strictly herbivorous species are found beyond 40° N and S latitudes (Horn, 1989). Herbivorous reef fish species in the subtidal habitats around New Zealand are the black angelfish *Parma alboscapularis*, parore *Girella tricuspidata*, bluefish *Girella cyanea*, silver drummer *Kyphosus sydneyanus*, marblefish *Aplodactylus arctidens*, notch-head marblefish *Aplodactylus etheridgi*, blue finned butterfish *Odax cyanoallix*, and *Odax pullus*. Most of these species have a very restricted distribution in New Zealand. *P. alboscapularis* is found predominately along the offshore islands of the north-eastern North Island and feeds mostly on fine red and green algae such as *Ulva*. *G. tricuspidata* and *K. sydneyanus* are northern species that can be very abundant locally. They feed on a mixture of fine filamentous seaweed, large brown algae and small invertebrates which may be taken incidentally (Ayling & Cox, 1982; Rimmer & Wiebe, 1987; Francis, 1988). Little is known about *G. cyanea*, which are most common at the Kermadec Islands and around the offshore islands of northern New Zealand. Bluefish are omnivorous fish which scrape seaweed and small invertebrates of the rocks (Francis, 1988). *A. etheridgi* is also restricted to the offshore islands but is never abundant. Some individuals occur around the exposed rocky headlands of eastern Northland and the Bay of Plenty (Ayling & Cox, 1987). *O. cyanoallix* are almost totally restricted to the Three Kings Islands and occur only rarely at Cape Reinga and the Poor Knights Islands. Similar to butterfish, they feed on large brown algae, such as the endemic *Sargassum johnsonii* (Choat & Schiel, 1982). The

herbivorous species that extend their range through southern New Zealand are the marblefish, *A. arctidens*, and butterfish, O. *pullus*.

Marblefish are a very inactive benthic species that feed mostly on fine red and green algae (Ayling & Cox, 1987). *O. pullus* is, therefore, the only mobile, herbivorous reef fish throughout most of New Zealand. Although its diet is dominated by fucalean and laminarian algae, it can also feed on a wide variety of other algae. Butterfish are highly specialised in their diet because of their ability to feed on fucoids which, although abundant in cold temperate waters, are rarely eaten by fish (Choat & Clements, 1992). These algae are rich in tannins and secondary metabolites, which can deter grazing (Estes & Steinberg, 1988; Gerking, 1994).

Making effective use of algae as the main dietary component requires special adaptations. Horn (1989) recognised four main types of digestive mechanisms based on the fundamental requirement that herbivores must rupture or break down cell walls to gain access to the nutrients inside the plant cells. Cell breakage can occur either by lysis, resulting from gastric acidity, or mechanical action, primarily from triturations in the pharyngeal jaws or a gizzard-like stomach (Lobel, 1981) or harbouring microbes that ferment the food in a hindgut or compartment (Horn, 1992). These digestive mechanisms occur in tropical and temperate reef fish.

Some fish species, such as the brown surgeonfish *Acanthurus nigrofuscus,* browse on soft red and green algae and have a thin-walled, acidic stomach (Montgomery & Pollak, 1988), using acid lysis to break down cell walls. The same digestive strategy is found in some temperate water species, such as the monkeyface prickleback *Cebidichthys violaceus* (Urquhart, 1984; cited in Horn, 1992). A thick-walled, muscular stomach, as found in some Muglilidae and Girellidae, serves mainly to triturate bacteria, diatoms and soft red and green algae. Therefore, fish with such internal organisation are usually grazers and feed predominantly on small filamentous algae and nutrient-rich particles in the sediment. Other species such as the redlip parrotfish

Scarus rubroviolaceus have developed a specialised pharyngeal apparatus which breaks down algal cell walls (Clements & Bellwood, 1988). The fourth type of digestive mechanism found in herbivorous fishes involves gut micro-organisms with the ability to process and digest cell walls (Horn, 1992). However, species must meet basic requirements, such as a constant food supply and prolonged gut transmit time, to maintain an efficient microflora (Bjorndal, 1987). Because a constant, preferably elevated, body temperature is another important factor for the culture of endosymbiontic gut communities, these processes may work more efficiently in warmer waters.

The specialised diet of butterfish, in combination with the perceived lack of obvious herbivorous specialisations (Horn, 1989), raises questions about how they digest seaweed. Butterfish differ from other herbivorous fish in their internal organisation. Most herbivorous fish have long intestines which aid in processing algae. Butterfish, however, have a short, simple intestine which is very similar to the labrid form. Their mean relative gut index (total gut length / standard length) falls within the range of some labrid species (Al-Hussaini, 1947). However their gut index is lower than the expected norm for a herbivorous species (Clements & Bellwood, 1988) which usually indicates limited herbivorous digestive ability.

Butterfish have an intestinal swelling rather than a stomach (Clements & Bellwood, 1988; Horn, 1989). They have an alkaline alimentary pH, and a pharyngeal apparatus capable of finely chopping but not masticating ingested algae (Clements & Bellwood, 1988; Clements, 1991). Clements (1991) indicated the presence of gut endosymbionts, similar to those found in termites that use fermentation as a means of digestion (To *et al.*, 1980). Whether microfloras play a role in the tolerance to, or detoxification of, chemically defended algae remains unclear (Horn, 1992). However, butterfish may use fermentative digestion to utilise macroalgae as food, as was suggested for kyphosids (Rimmer & Wiebe, 1987). Overall, very few species have acquired these adaptations in cold temperate waters, which is an indication of the

many physiological requirements for cold water herbivory.

Butterfish have the ability to maintain a herbivorous diet at high latitudes (Choat & Clements, 1992). This indicates the unique patterns of food processing and assimilation, as well as their adaptive abilities to latitudinal differences in seaweed abundance. Seaweed abundance and distribution vary considerably between the southern and northern parts of New Zealand (Schiel, 1990). These latitudinal differences in algal assemblages are reflected in the different diets of *O. pullus* from different areas. Butterfish in northern New Zealand feed predominately on *Ecklonia radiata* and *Carpophyllum* spp. which are the dominant species in those warmer water habitats. Further south, *Lessonia variegata* rather than *E. radiata* is the major component of the laminarian biomass (Schiel, 1990). This latitudinal change in algal abundance is reflected in the diet of *O. pullus*. Around Kaikoura, butterfish feed predominantly on *L. variegata* which is very abundant in the subtidal habitats (Chapter 4). Although the fronds of *Lessonia* are generally tougher than those of *Ecklonia* this seems to present no difficulties to *O. pullus* in their feeding activities.

Because of their great abundance in some areas, marine herbivores have been suggested to be a major structuring agent of algal assemblages. Herbivorous fish species associated with coral reefs appear to have a major impact on the abundance of algae (Scott & Russ, 1987). Not only are there many herbivorous species on coral reefs but many of these can be very abundant, exerting considerable grazing pressure on localised areas. In temperate rocky reef habitats, however, even though herbivorous fish can be greatly abundant, their effects on the structure of algal communities are still largely unknown. Jones (1992) suggested that temperate herbivorous fishes play less of a role in modifying algal distributions than their tropical counterparts, partly because of the over-riding influence of kelp on the distribution of fish and their food algae. Choat & Ayling (1987) concluded that it is the characteristics of the habitat that determines the nature of the fish fauna on reefs, rather than the reverse. In the case of *O. pullus*, they are so widespread over a reef that their effects

may be more dispersed than those of tropical fish.

Because most temperate herbivorous fish show unique feeding characteristics, grazing may be of localised importance. For example, Andrew & Jones (1990) showed that herbivory by *Odax cyanomelas* had a great effect the structure of *Ecklonia radiata* forests, which occurred in small patches along a reef at a site near Sydney, Australia. The feeding of *O. cyanomelas* concentrated on the secondary laminae of *E. radiata* and browsing damage was so severe that approximately 30% of all plants within the forests died. However, the algal beds tended to replace themselves annually because the die-off coincided with pulses of *Ecklonia* recruits. This is one of the only studies to demonstrate a community effect of fish grazing in temperate marine areas. Meekan (1986) concluded that because of marked spatial and temporal variability in the feeding of *O. pullus*, this species was unlikely to have a major effect on the dynamics of *E. radiata* populations in New Zealand waters. However, because of the marked latitudinal differences in the abundance of butterfish, impacts on algal assemblages may be more severe in highly populated areas. Furthermore, male *O. pullus* are territorial, at least for part of the year, and their feeding may be concentrated on small parts of kelp beds.

During this study there was no indication that butterfish populations had a structuring role in subtidal algal assemblages around the Kaikoura Peninsula. However, the degree to which herbivorous feeding by *O. pullus* may contribute to long-term patterns of the abundance of local algal assemblages is still uncertain. The relative importance of this interaction also appears to be linked to other factors, such as available recruitment, physical disturbance, grazing by other herbivores and plant-plant interactions (Andrew & Jones, 1990).

O. pullus are very active fish, with older individuals showing almost continuous swimming behaviour (Chapter 5). Choat & Clements (1993) estimated the daily movement rate of butterfish to be considerably greater than that estimated for other

cold-water herbivorous fish, such as the monkeyface prickleback *Cebidichthys violaceus*. Clements (1985) recorded movements of individual *O. pullus* of around 300 m in less than 30 minutes whereas *C. violaceus* was shown to travel only distances of around two metres within the 40 min observation periods (Ralston & Horn, 1986). Maintaining these high activities again indicates the unique ability to process laminarian and fucoid algae and to extract the necessary energy.

6.3. Conclusion

Odax pullus is one of the most common reef fish around New Zealand. Its specialisation in herbivory makes it uniquely suited to take advantage of an abundant and continuously replenishing food source, the forest of laminarian and fucalean algae. Butterfish can clearly utilise different foods as they change over the latitudinal gradient of New Zealand. Although little is known about spawning behaviour, it seems clear that *O. pullus* has a complex social system, having large males and large females . Around Kaikoura, it seems likely that courtship displays and spawning occur either in open water or deep reefs, as ritualistic behaviour has never been seen. Butterfish have only a moderate life span for an inshore mobile reef fish (9 - 10 years), yet populations seem to be robust around the Kaikoura Peninsula, despite intense fishing.

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APPENDIX ONE

Species Codes

A. Fish species and algal taxa

Code	Species	Common Name
BCO	*Parapercis colias*	Blue Cod
BPF	*Notolabrus fucicola*	Banded Wrasse
BUT	*Odax pullus*	Butterfish
GPF	*Notolabrus cinctus*	Girdled Wrasse
GTR	*Aplodactylus arctidens*	Marblefish
LEA	*Parika scaber*	Leatherjacket
MOK	*Latridopsis ciliaris*	Blue Moki
RMO	*Cheilodactylus spectabilis*	Red Moki
SPF	*Pseudolabrus miles*	Scarlet Wrasse
STY	*Notolabrus celidotus*	Spotty
TAR	*Nemadactylus macropterus*	Tarakihi
YEM	*Aldrichetta forsteri*	Yellow-eyed Mullet

Code	Species
MG	*Marginariella boryana*
MC	*Macrocystis pyrifera*
LA	*Landsburgia quercifolia*
CA	*Carpophyllum* spp.
LES	*Lessonia variegata*
EKL	*Ecklonia radiata*
RS	Red seaweeds
GS	Green seaweeds
Other	*Landsburgia quercifolia* *Cystophora torulosa* *Sargassum sinclarii*

B. Animal matter

Code	Description
SP	unidentified sponge material
SB	Shells of unidentified bivalves
SN	shells of unidentified snail species
SO	snail operculs
BR	Bryozoa
GA	*Gammarus* spp.
NU	nudibranchs
FE	fish eggs
SA	Thaliaceae (Salps)
MY	fragments of *Mytilus* spp.